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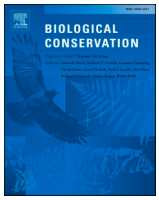
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Impacts of logging, hunting, and conservation on vocalizing biodiversity in Gabon

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ABSTRACT

Tropical forests support two-thirds of the world's biodiversity, contribute to global climate regulation, and support the culture and livelihoods of forest-dependent people. Much of extant tropical forest is subject to selective logging and hunting - extractive activities that potentially alter ecosystem function and species diversity. However, the collective impact of these threats, especially in the context of protected vs unprotected areas, is not fully understood. Here we assess how vocalizing biodiversity responds to logging and hunting, across the diel cycle, seasonally, and between protected and unprotected landscapes in Gabon. We compared soundscape saturation across 109 sites in national parks, Forest Stewardship Council (FSC) certified, and non-certified logging concessions. We estimated hunting pressure by quantifying gunshots and relative accessibility per site. Overall, we found that the soundscapes of FSC-certified concessions resembled national parks (selectively logged 20+ years ago) more so than non-certified concessions. We also found that never logged sites, part of a proposed community conserved area, had different soundscapes than all other categories, including national parks. Unlogged sites had higher saturation than logging concessions at dusk and dawn. Soundscapes and hunting pressure were highly variable across different concessions. We found that higher gunshot rates and recent logging were associated with lower soundscape saturation overall. Based on our findings, we recommend that (i) the very few never logged forests that remain (and are not yet protected) should be urgently withdrawn from selective logging, and (ii) FSC or other certification schemes should be promoted in Gabon, with an emphasis on sustainable hunting.

1. Introduction

Tropical forests are important to people at multiple spatial scales (Chazdon et al., 2016; Edwards et al., 2019). Locally, forests can often be the main source of protein and income from wild meat, provide natural resources for resident communities and Indigenous Peoples, as well as represent places of cultural significance (Asprilla-Perea and Díaz-Puente, 2019; Van Gils et al., 2019). Nationally, tropical forests can be an important source of revenue from selective logging and ecotourism (Barbier et al., 2021). Globally, tropical forests are one of Earth's largest carbon stores (25 % of terrestrial carbon) and support a disproportionate amount of biodiversity (e.g., 96 % of all tree species, >50 % of terrestrial

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vertebrates), which contributes to the provision of ecosystem services (Bonan, 2008; Fine et al., 2008; Mitchard, 2018; Pillay et al., 2022).

Forest certification schemes, such as the Forest-Stewardship Council (FSC), the Programme for the Endorsement of Forest Certification – Pan African Forest Certification (PEFC-PAFC), and sustainable community forest schemes, among others, aim to reduce negative effects of selective logging on forests and people by promoting forest management that is socially, environmentally, and economically sustainable, including species conservation (FSC, 2020; Trolliet et al., 2019). As of 2018, approximately 20 % of the world's production forests were certified under FSC and PEFC worldwide, but far fewer tropical production forests have obtained certification (Cubbage and Sills, 2020). Compared to non-certified logging, FSC-managed forests are associated with less environmental harm and greater positive social impacts such as safer working conditions and increased education opportunities (Buřivalová et al., 2017; Cerutti et al., 2014, 2017). Camera trapping and aerial imagery surveys indicate that certification maintains more biodiversity than conventional logging, however, such surveys are still limited and taxonomically biased towards mammals (Imai et al., 2009; Sollmann et al., 2017; Wolff and Schweinle, 2022; Zwerts et al., 2024). Importantly, the challenge is often to disentangle the effects of improved logging practices from other management interventions associated with forest certification, such as more strongly regulated hunting (Poulsen et al., 2011).

Unsustainable hunting can exacerbate the negative effects of land use change on forest biodiversity, leading to further species extirpations, population declines, disruption to ecosystem functioning, and reduced forest resilience (Benítez-López et al., 2019). However, hunting, wild-meat consumption and trade are often important to people's diets, livelihoods, and culture (Harrison, 2011; Ingram et al., 2021; Lamperty et al., 2020). Conservation efforts that restrict hunting, such as strict protected areas, can therefore conflict with local resource use and are often ignored without additional community engagement or enforcement (Borgerson et al., 2019).

Protected areas are a cornerstone of conservation (Watson et al., 2014). The Kunming–Montreal Global Biodiversity Framework (GBF) builds on the Strategic Plan for Biodiversity Aichi Target 11 and calls for at least 30 % of the Earth's surface to be designated as protected or conservation areas (i.e. other effective area-based conservation measures) by 2030 (CBD, 2022). However, protected areas can have negative social and economic impacts where they do not incorporate local community forest use and culture (Büscher and Fletcher, 2020; Watson et al., 2014). Moreover, without effective management and resourcing, so-called “paper parks” do not guarantee conservation benefits.

A critical question for tropical forest conservation globally is how logging, hunting, and protected areas - individually and collectively - affect biodiversity. Most nations with tropical forests grapple with the trade-offs between managing forests for local subsistence and conservation, economic growth, and global climate and biodiversity goals. Despite the interplay between logging, hunting, and protected areas, few studies have quantified their impact in the same framework for forest fauna (Brodie et al., 2015; Poulsen et al., 2011). This is often due to the challenges of surveying fauna in tropical forests under different land designations, while simultaneously monitoring human behavior which may be socially sensitive depending on the context (e.g. if hunting is illegal/taboo).

Remote sensing, including LiDAR, camera traps, and acoustic sensors, can be used to systematically monitor the effectiveness of area-based conservation measures and the impact of other land uses over large geographical and temporal scales (Campos et al., 2021; Visconti et al., 2019). Monitoring soundscapes (all sounds in a landscape) allows us to monitor biodiversity at multiple sites, across multiple taxonomic groups, across multiple land-use types (Dröge et al., 2021; Gibb et al., 2019; Pijanowski et al., 2011; Ross et al., 2018). Moreover, recording soundscapes can detect potential threats to biodiversity, such as gun hunting (Astaras et al., 2020; Hedley et al., 2022; Katsis et al., 2022). Therefore, soundscapes can be used to monitor both fauna that produce sound (vocalizations, stridulations) and audible human impacts (gunshots, logging operations, etc.) and they are well suited to a low visibility environment, such as tropical rainforests.

Here, we use soundscapes to understand the impacts of hunting, logging, and protected areas on biodiversity in Gabon. Gabon is one of the most forested countries in the world with approximately 91.3 % tree cover (Global Forest Watch, 2024). Locally, people rely heavily on forests to hunt and fish (Froese et al., 2022; Wilkie et al., 2019). Nationally, >50 % of Gabon's forests are leased to (mostly internationally owned) logging companies, contributing substantially to the GDP (Buřivalová et al., 2022). Globally, Gabon is often considered a leader in forest carbon conservation within the Congo Basin (Poulsen et al., 2020). With biodiversity conservation as a goal, in 2002 Gabon established thirteen new national parks, protecting approximately 10 % of the country's land (Yobo and Ito, 2016). To understand the collective impact of logging, hunting, and protected areas, we quantify hunting pressure from gunshot detections and accessibility measures, and logging impact from ground and remote sensing observations. Then, we assess whether soundscapes differ among forest designations (national parks, a proposed community conserved area, FSC-certified and conventional, non-certified logging concessions). Finally, we test whether observed differences are due to logging, hunting, or both.

We predict that soundscapes in national parks and the proposed community conserved area will have the highest soundscape saturation, particularly during the peak times of vocalizing activity, i.e. dawn and dusk. This is because we hypothesize that logging and hunting disturbance would lead to reductions in the number of vocalizing birds and mammals typically active during these times. We do not expect hunting and logging disturbance to necessarily reduce soundscape saturation overall, as previous studies found nocturnal insect sounds increase in logged sites (Buřivalová et al., 2020; Campos-Cerqueira et al., 2020). We predict that FSC-certified logging will change soundscapes less than non-certified logging, which we expect will have the lowest soundscape saturation. This is because we predict hunting and logging disturbance to be lower in FSC-certified concessions due to hunting restrictions and stricter adherence to Reduced Impact Logging techniques.

2. Methods

2.1. Study area

Between February 2021 and June 2022, we sampled soundscapes at 110 sites across Gabon (Fig. 1). Gabonese forests are highly diverse, for example over 418 bird species have been recorded in Ivindo National Park alone (Abitsi et al., 2013; Sassen and Wan, 2006). All our study areas are important habitats for the critically endangered forest elephant (*Loxodonta cyclotis*) and the western lowland gorilla (*Gorilla gorilla gorilla*). Gabon has an equatorial climate with consistently high temperatures (22–27 °C) and humidity across the year. Our sampling covered the main dry (May to September; 37 sites) and rainy season (October to April; 73 sites) to account for seasonality (Mahé et al., 1990).

We sampled soundscapes in four of Gabon's nine provinces: the Ogooué-Ivindo, Ogooué-Lolo, Nyanga, and Ngounié. In each province, we sampled three different land use designations: national parks (Ivindo, Lopé, and Moukalaba-Doudou National Parks, 41 sites total), FSC-certified selective logging concessions (anonymized, 32 sites in 3 concessions), non-certified selective logging concessions (anonymized, 32 sites in 3 concessions). Additionally, we sampled in a proposed community conserved area, Ibola Dja Bana Ba Massaha, in the Ogooué-Ivindo province (5 sites, hereafter referred to as the PCCA). The sites sampled in the PCCA were in an unlogged area of forest situated within a non-certified concession. During our study, the legal status and designation of this land were being determined.

Our sites included two main habitat types present in our study area:

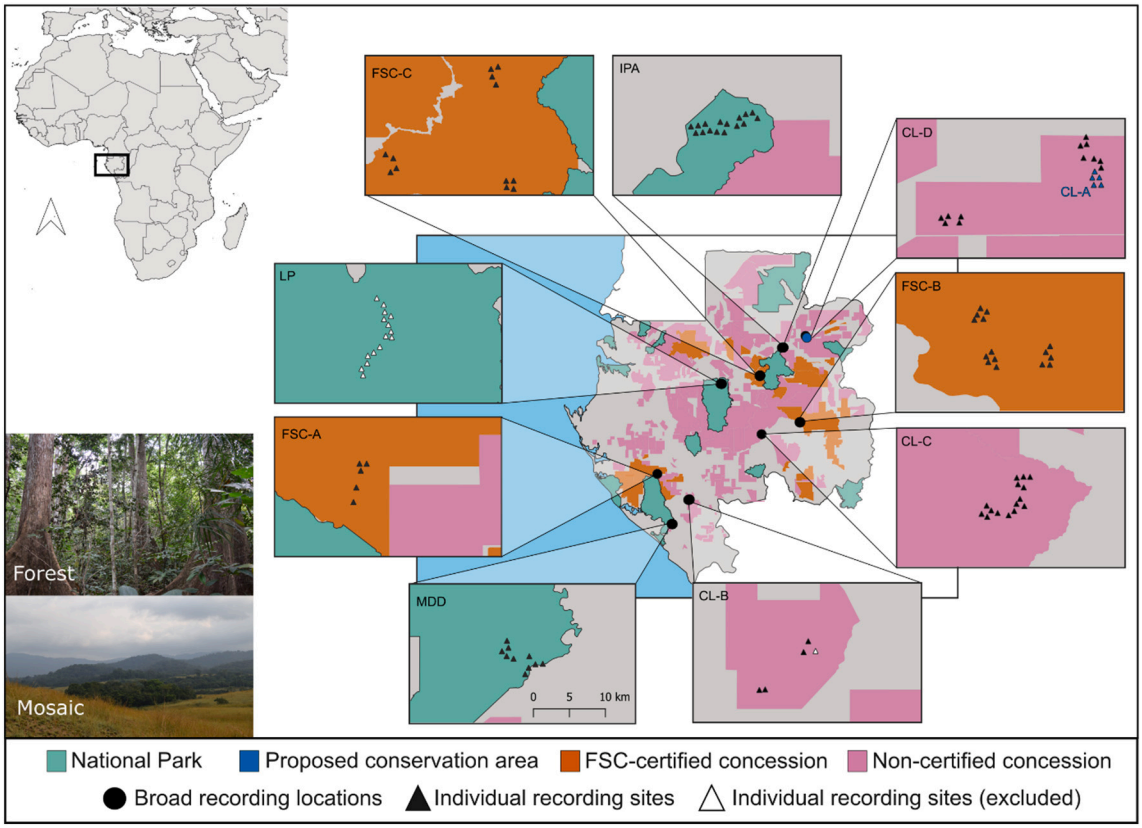


Fig. 1. Map of the recording locations within our study region in Gabon, Central Africa (inset), within each of the color-coded forest designations (Table S1). The blue point represents the proposed community conservated area (PCCA) within a non-certified logging concession. The white triangles represent sites which were excluded from the analysis. More information regarding sample sites is available in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Data for the location of National Parks retrieved from UNEP-WCMC and IUCN (2023).

closed rainforest (hereafter referred to as 'forest'), and forest-savannah mosaic ('mosaic'). Sampling sites within the mosaic were situated within forest patches at least 200 m from the forest edge (Broadbent et al., 2008). Umunay et al. (2019) reported timber extraction volumes between 22 and 56 m^3 ha^{-1} per hectare for logging concessions across Gabon. FSC-certified concessions differed from non-certified concessions by logging practices and hunting regulations, among others. For example, in Gabon, FSC certification requires the following criteria to be met: a limitation on the number of trees felled per hectare, buffer areas around major rivers, security gates on main forest roads, road closure post-harvesting, efforts to avoid soil compaction, surveillance patrols to prevent hunting, safer working conditions, and providing workers with alternative forms of protein, among others (Forest Stewardship Council, 2020). The national parks we sampled had previously been part of logging concessions before being established around 2002 and had been selectively logged approximately 20–40 years prior to sampling. Hunting and logging are illegal in the parks. Tourism was generally limited in Gabon but was extremely limited during our study period given the COVID-19 pandemic.

2.2. Acoustic sampling

We deployed multiple bioacoustic recorders to quantify the soundscape within each forest designation, separating sampling sites by at least 1 km to ensure independence. Under specific conditions, forest elephants (likely the species with the longest-ranging sounds in our study area) in Ivindo National Park can communicate across several km. However, most calls attenuate at just 0.1 to 0.8 km under average ambient sound levels (Hedwig et al., 2018). Therefore, we consider our sites independent for the majority of biological sounds. At each site, we deployed one Bioacoustic Recorder (BAR-LT, Frontier Labs) at 1.8 m above ground with a single omnidirectional microphone pointing down, as a compromise between limiting exposure to rain and capturing a broader array of sounds. Recorders were programmed for continuous, autonomous recording in 30 min segments for at least seven days per site (Bradfer-Lawrence et al., 2019). We only included complete days in the final analysis (e.g. 1440 min per day; mean no. days per site = 5.8 ± 2.0). Partial days could result from recording errors or days of deployment and retrieval. Deployment dates and days per site are provided in Table S1. We recorded soundscapes at 40 dB gain and 44.1 kHz sample rate. Within the concessions, sampling sites were located at least 200 m away from the nearest main logging road and not directly in a clearing created by logging. All logging operations had concluded in the cutting blocks before sampling began. In national parks, we positioned sites at least 200 m from retired logging roads, ridgeline foot trails, and rivers (Table S1). Both measures were taken to avoid accidentally capturing human voices and attracting human attention.

2.3. Site characteristics

For each site, we derived variables from site observations during BAR-LT deployment and from spatial layers (Table 1; Table S1).

2.3.1. Logging disturbance

We measured changes in the forest due to selective logging in three ways. First, we used the global forest loss dataset (V1.9) from Hansen et al. (2013) to calculate forest extent at the time of our surveys (for sampling during 2021, we calculated forest cover for 2020, etc.).

Table 1
Summary of the main site characteristics by forest designation, forest type, and season. PCCA – proposed community conserved area. Dist. – Distance; Can. – Canopy. Site summary excludes CL-B5 and Lopé NP as these were not used in the analyses.

Forest designation	Forest type	Season	N sites	N days	Gunshot rate (daily)	Dist. to village (m)	Dist. to river (m)	Dist. to road (m)	Can. height (m)	Forest extent (%)
National Park	Forest	Rainy	16	107	1.12 (±0.61)	7903 (±2288)	4952 (±2211)	3252 (±1330)	26.4 (±2.2)	99.8 (±0.3)
National Park	Mosaic	Dry	10	80	0.11 (±0.17)	15,593 (±1661)	1651 (±1204)	1261 (±875)	23.5 (±5.9)	77.8 (±25.7)
National Park	Mosaic	Rainy	15	78	0.02 (±0.07)	7638 (±2997)	5895 (±3028)	189 (±176)	16.8 (±4.8)	35.9 (±23.3)
PCCA	Forest	Dry	5	32	1.03 (±0.37)	7317 (±712)	1052 (±454)	2632 (±705)	28.3 (±0.4)	100.0 (±0.0)
FSC-certified logging	Forest	Dry	12	80	0.09 (±0.12)	11,175 (±5286)	3243 (±1360)	601 (±388)	31.5 (±1.5)	96.3 (±6.9)
FSC-certified logging	Forest	Rainy	15	65	1.31 (±1.11)	14,741 (±2065)	6852 (±1515)	921 (±567)	25.9 (±1.2)	99.4 (±0.9)
FSC-certified logging	Mosaic	Dry	5	39	0.32 (±0.09)	3924 (±2052)	10,179 (±1756)	537 (±135)	28.7 (±2.1)	100.0 (±0.0)
Non-certified logging	Forest	Dry	4	28	1.27 (±0.67)	7066 (±2270)	13,718 (±930)	1268 (±878)	31.6 (±2.5)	100.0 (±0.0)
Non-certified logging	Forest	Rainy	27	122	1.20 (±0.58)	5172 (±2042)	3768 (±2114)	547 (±422)	27.9 (±2.5)	99.8 (±0.6)

Although selective extraction of trees does not typically lead to forest loss at a spatial scale visible on Landsat satellite images, selective logging can lead to deforestation through the development of wider logging roads, log landings, and other infrastructure, detectable through this step (Fig. S1). Therefore, forest extent is not a measure of forest degradation, but coverage. We reclassified pixels using a 60 % threshold to classify sites as forest (≥ 60 %) or non-forest (< 60 %) (Shennan-Farpón et al., 2021). The proportion of forest cover (*forest extent*; continuous) was subsequently calculated for a 300 m buffer around our sampling sites using the R package *raster* (Hijmans et al., 2023). Ultimately, *forest extent* reflected *forest type*, rather than observed differences in vegetation related to forest designation (Fig. S2). Therefore, we did not include it in the final modelling as this was already expressed by the variable *forest type* (mosaic or forest).

Second, we documented the logging history at each site as specified in forest management maps and logging crews as *years since logging.* As these were provided as ranges of several months, we aggregated the data into three categories in the final modelling (logged <2 years ago, logged 20+ years ago, never logged). Third, we calculated mean *canopy height* at 300 m using a raster from remote sensing as a measure of forest quality. We developed a country-wide forest canopy height map by combining Sentinel-1 backscatter and Sentinel-2 vegetation index images with GEDI satellite-based LiDAR data using multiple machine learning algorithms (Dubayah et al., 2020). The accuracy of the canopy height map had an error rate of four meters (10–15 %) Root-mean-squared-error.

2.3.2. *Hunting pressure: gunshot detection*

Unlike forest loss, hunting is nearly undetectable using remote sensing (Peres et al., 2006). Therefore, hunting pressure is often monitored through participatory surveys, such as hunter-recall interviews or village-based monitoring approaches. However, such approaches suffer from different biases depending on cultural factors and the socioeconomic context and are time-consuming (Froese et al., 2022; Ibbett et al., 2022; Jones et al., 2020). In Gabon, although hunting unprotected species is theoretically possible, depending on the method, season, offtake, time of day, use, etc. (The Forest Code, 2001, 2007), almost all practised hunting is illegal but hunting regulations are rarely enforced. A wide range of species are hunted, including ungulates, primates, rodents, reptiles, and birds; both for local consumption and for sale (Froese et al., 2022, 2023). The erosion of community governance in favor of national hunting regulations, combined with the modernization of hunting methods, is thought to have increased hunting and the availability of wild meat for sale at urban markets (Walters et al., 2015). See Froese et al. (2022) for more information on the legal and cultural context of wildmeat hunting in our study area.

We estimated hunting pressure in two ways. First, we quantified the number of gunshot sounds detected at each site during the recording period. This approach can be used so long as guns are a dominant hunting strategy (Hedley et al., 2022; Katsis et al., 2022). At our Ogooué-Ivindo study site, Froese et al. (2022) found that 71 % of all hunted animals were shot versus trapped. We used a convolutional neural network model to identify gunshots from our acoustic recordings. To train and test our model we used *Koogu* v0.7.1, an open-sourced Python package for developing machine learning models for bioacoustics (Madhusudhana, 2022; Madhusudhana et al., 2022). We employed a 3-step process to collate a library of gunshot and non-gunshot sounds. First, we scanned through a random subset of 1000 recordings and identified multiple gunshot sounds. Second, we built a template detector using these gunshot sounds in R with monitoR (Katz et al., 2016) and evaluated the output in Raven Pro 1.65 Sound Analysis Software (K. Lisa Yang Center for Conservation Bioacoustics, Ithaca, NY). This step yielded 361 gunshot sounds and 8614 non-gunshot sounds. Third, we built a preliminary Koogu model, using 223 of the gunshot sounds for training and 138 for testing, which detected an additional 203 gunshots. To improve the model recall, we added these additional gunshots to the original training dataset and retrained the model. However, sixteen gunshot annotations were excluded due to Koogu's handling of the selection table and sound matching. Consequently, the final training dataset consisted of 410 gunshot examples and 8614 non-gunshot sounds (e.g. branch snaps, tree falls, calls of the putty-nosed monkey *Cercopithecus nictitans*, ambient noise; see SI for additional details on model architecture).

We evaluated the precision and the recall across confidence scores and selected a confidence score threshold of 0.9 to obtain a recall of 0.95 and a precision of 0.89. We then ran the model on the full dataset which generated 6818 detections. We manually reviewed all detections in Raven Pro and gave each detection a score ranging from 0 to 5 (0 = definitely not a gunshot, 5 = definitely a gunshot). We only included gunshots with a confidence score of 4 or 5 in subsequent analyses. The model precision decreased to 0.09 across the full dataset because there were gunshot-like sound types that were not well-represented in the training data, including sounds from owls, chimpanzees, humans talking, thunder, and certain ambient noise environments that resembled the tail of a gunshot (Katz et al., 2016). We are confident that the recall remained near 0.95 over the full dataset because the training dataset captured the variability of gunshot sounds at these sites and a manual review revealed just one false negative. It is worth noting that gunshot detectability typically declines with distance from the source, as gunshots become indistinguishable from sounds of snapping branches and falling fruit. This challenge in identifying distant gunshots likely led to false negatives during the human scoring step, which was a necessary compromise to exclude false positives from the dataset. The code and anonymized training data are available via Zenodo (see Data

Availability Statement).

2.3.3. Hunting pressure: accessibility

In addition to gunshot detection, we produced a spatially explicit *accessibility* layer to estimate the spatial variability in hunting effort, providing a rough proxy for silent forms of hunting (e.g., snares/traps) and to help mitigate imperfect detection. We derived accessibility using the Distance Accumulation tool in ArcMap Pro 2.9.0 (ESRI, 2022) by calculating the relative speed a person could travel to each sampling location based on Tobler's hiking function using settlements as potential starting locations. With this approach, the person's speed is mediated by the degree of slope and features which can aid or impede movement, such as roads and rivers. Data for settlements, rivers, and roads were retrieved from OpenStreetMap (Humanitarian OpenStreetMap Team, 2022a, 2022b, 2022c). We amended data layers for settlements and rivers based on personal observations in the field, e.g., to exclude roads which are no longer operational or rivers not suitable for navigation. We assigned rivers and each road type a corresponding travel time based on in-country speed limits and travel speeds estimated in similar analyses (Table S2). We derived slope from a 30 m digital elevation model (Farr et al., 2007). The final metric was scaled and inverted so the resulting metric is unitless, where the higher the relative accessibility the more accessible the sites.

2.4. Acoustic data processing

2.4.1. Acoustic indices

Manually identifying individual species from the soundscape in tropical forests can be extremely challenging and time-consuming (Sun et al., 2022). Species-specific automated classifiers can reduce identification time but these are unavailable for most tropical species, especially in the Afrotropics (Zwerts et al., 2021). Acoustic indices provide an alternative approach by estimating differences in soundscape characteristics as a proxy for changes in ecological communities, without the need to classify individual sounds. There are now over 69 different acoustic indices which use time, frequency, and energy to summarize the complexity or heterogeneity of sound (Buxton et al., 2018; Sueur et al., 2014). While acoustic indices do not necessarily reflect the true alpha diversity of a given location or generalize between regions (Sethi et al., 2022), a meta-analysis by Alcocer et al. (2022) found they can be effective for capturing changes in the relative abundance of sounds and therefore comparing different ecological states.

First, we calculated the index Power Minus Noise (PMN) for 256 frequency bins between 0 and 11 kHz (~43 Hz bandwidth each) using Ecoacoustics Audio Analysis Software v21.7.0.4 (Towsey et al., 2020), following Towsey (2017). An upper range of 11 kHz captures most vertebrate vocalizations, excluding bats. Next, from PMN, we derived the index soundscape saturation, which reflects the proportion of frequency bins per minute that are acoustically active (at a threshold of 1.5 dB), as defined in Buřivalová et al. (2018). Soundscape saturation, calculated for each minute, operates under the assumption of the acoustic niche hypothesis that species have evolved to minimize how their vocalizations overlap to decrease signal interference (Krause, 1993). As such, it is assumed to provide an intuitive proxy for vocalizing species richness. Previous studies have shown soundscape saturation can be effective for monitoring changes in biodiversity in tropical forests, including in Gabon (Buřivalová et al., 2018, 2019, 2020; Zwerts et al., 2022).

2.4.2. Sonotype richness

To verify whether soundscape saturation provides a meaningful proxy for vocalizing diversity in our study location, we tested the relationship between overall soundscape saturation and the number of sonotypes per minute for a subsample of the recordings. A sonotype is defined as a unique sound or "a note or series of notes that constitute a unique acoustic signal" (Aide et al., 2017). We quantified the number of sonotypes between 0 and 11 kHz for 1 min per hour for four sites (92 min in total). We chose one site from a national park, proposed community conserved area, and both logging concession types to validate the index across designations. The minute was chosen at random for each site but remained consistent within a site, such that if the randomly selected minute for site A was 13, we would sample minutes 0:13, 01:13, 02:13, …, 23:13. For each minute, we manually annotated all animal vocalizations in Raven Pro, assigning them to a corresponding sonotype. Individual sounds of the same sonotype that were over 2 s apart were labelled separately. We subsequently used linear regression to compare the relationship between the number of sonotypes per minute and the corresponding value for soundscape saturation. Other studies which have done a similar comparison reported significant relationships and adjusted r-squared between 0.25 and 0.35 (Buřivalová et al., 2019; Gottesman, 2019; Zwerts et al., 2022).

2.5. Statistical analysis

We applied generalized additive models (GAMs) to determine how soundscapes varied among forest designations across the day, between seasons, and in response to disturbance. We chose GAMs over other models as we expected soundscape saturation to exhibit a nonlinear relationship response to predictor variables across the day (Lawson et al., 2022). Many variables could affect soundscape saturation, including *forest-designation* (categorical; "National park", "PCCA", "FSC-certified logging", "Non-certified logging"), *forest type* (categorical: "Forest", "Mosaic"), *accessibility* (continuous), *canopy height* (continuous), *year since logging* (ordinal; "Less than two years", "Twenty + years", "Never logged"), *season* (categorical, "Dry", "Rainy"), and *daily gunshot rate* (continuous). Due to real-world constraints, we could not sample all combinations of factors. Therefore, we subset the data into four comparison groups to isolate variables of interest and rule out the impact of imperfectly sampled covariates (Fig. 2). These groups were (1) all mosaic sites in the dry season (n sites = 15), (2) all forested sites in the rainy season ($n = 58$), (3) all forested sites in the dry season ($n = 21$), and (4) forested FSC-certified concession sites in both seasons ($n = 27$).

Using groups 1–3, we first assessed how soundscape saturation differed between forest designations. To do this, we created two GAMs for each group. In the first, simpler model, we included a smoothing term to model time of day, whereas in the second model, we included an interaction term for smoothing between time of day and forest designation. We compared model performance to test whether temporal effects differed among forest designations (independent of season or habitat). We repeated this approach for group 4 to assess whether there was a seasonal effect on soundscape saturation (Table S3).

Next, we investigated the likely mechanisms for the differences observed. To do this, we used data from group 2 (all forested sites in the rainy season) to build additional, hypothesis-driven models to assess separately how (i) logging and (ii) hunting disturbance impact soundscape saturation. This is necessary because formally designated forest use types do not always correspond to levels of logging and hunting as one might assume (for instance, hunting may occur within a national park). Due to the nature of logging and hunting across the landscape, few sites in each forest type could be compared in terms of logging while investigating the impact of hunting, and vice versa. Therefore, we chose to further subset the data used to examine the impact of hunting to only sites logged 20 or more years prior (group 5; n sites = 25; Table S3). Due to the distribution of the data, we used all sites from group 2 to investigate the impact of logging. Overall, although dividing sites into subgroups limits the comparisons we can make, the answers that we do get are much more robust than if using the whole dataset, as we are comparing "like with like".

In all models, continuous variables were fitted as smoothing terms or linear terms to determine which were most appropriate for the final model using Akaike Information Criteria (AIC). Models included *forest-designation* as both a categorical predictor and as an interaction term

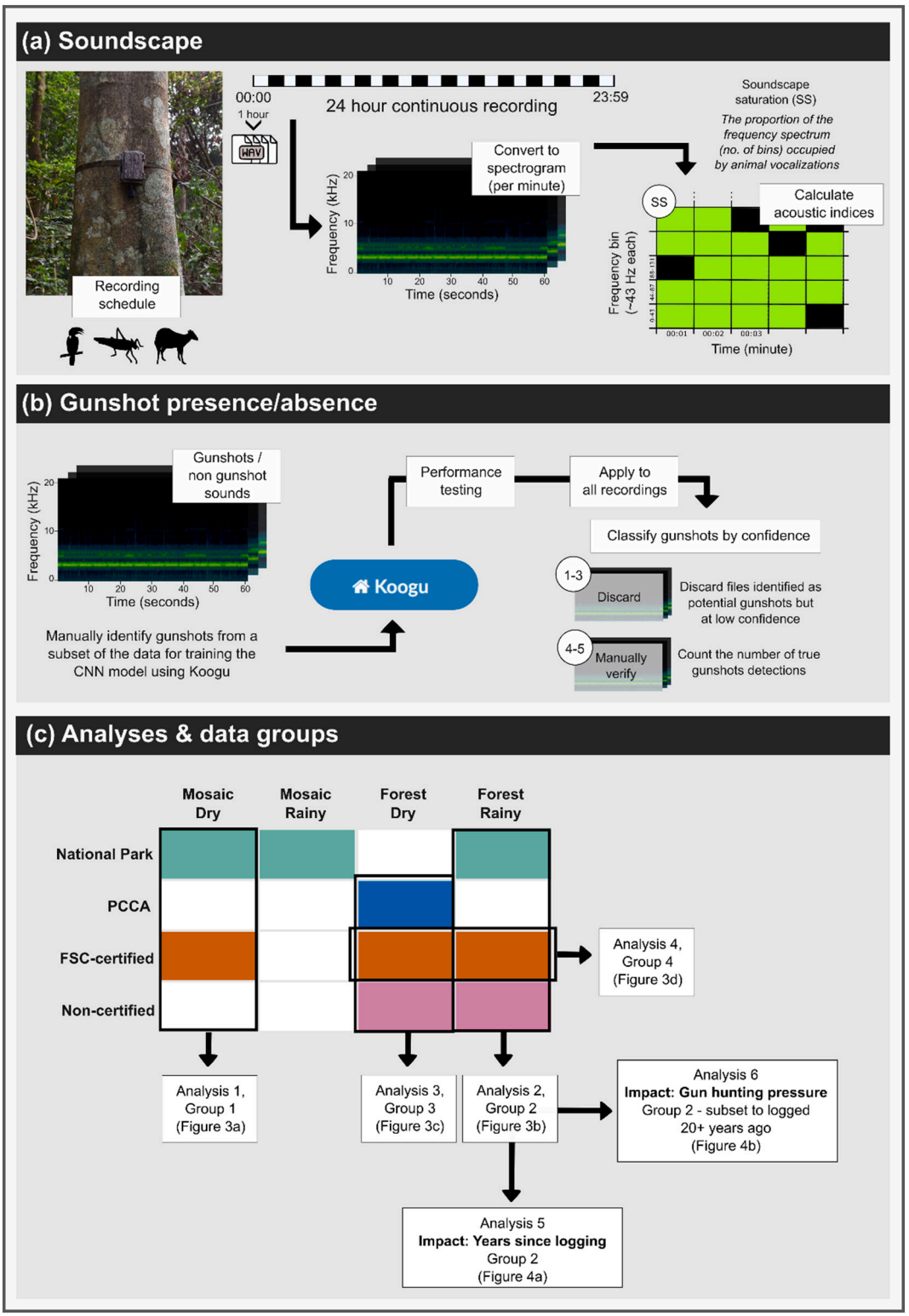


Fig. 2. Methodological framework to assess the impacts of logging, hunting, and protected areas on the soundscape, including (a) details of soundscape sampling; (b) process for quantifying gun hunting, and (c) how the data was subset between analyses. Models used were generalized additive models. PCCA – proposed community conserved area. FSC-certified and non-certified represent two types of selective logging concession.

with time. Models were fitted with a Gaussian distribution with an identity link function using the *mgcv* package (Wood, 2023). Before model fitting, outliers identified using the *boxplot.stats* function in base R were removed to improve model fit. We centered and scaled continuous covariates to one-unit standard deviation and assessed for collinearity using Pearson correlation coefficient. There was a Pearson correlation coefficient of $|r| \leq 0.7$ between the final covariates. The restricted maximum likelihood method was used for smoothness selection and the degree of smoothing was tested by fitting different basis functions and assessing fit, both visually and using AIC. The final model performance

was evaluated using AIC to select the model with the best fit (< 2 ΔAIC). We used the final model to predict soundscape saturation for each data group. We also predicted soundscape saturation in response to years since logging and hunting pressure (as described by *daily gunshot rate*). Predictions were generated for both types of logging concession and national parks in forest and the rainy season where all non-target covariates were standardized to the mean. All analysis was performed using R version 4.2.1 (2022-06-23) statistical software.

3. Results

In total, we recorded 15,264 h or 636 days of soundscapes across 109 sites. We found that soundscape saturation differed seasonally among forest designations in both forest and mosaic forests across the diel cycle (Fig. 2; Table S4).

3.1. Forest designation

On average, non-certified concessions had the lowest soundscape saturation in both seasons compared to all other forest designations (Fig. 3b,c). We also observed considerable differences in the behavior of the soundscape between closed and mosaic forest (Fig. 3a and c). FSC-certified logging had lower soundscape saturation compared to national parks during most of the day in mosaic and forest sites. The never logged forest sampled, i.e. the PCCA, had higher soundscape saturation than both concession types before dawn and during dusk (Table S4; Fig. 3c). Soundscape saturation in FSC-concessions was higher throughout the day in the rainy season compared to the dry season (Fig. 3d; Table S3).

The dawn peaks in soundscape saturation were more pronounced in FSC-concessions compared to the national park in the mosaic forest for the dry season (Fig. 3a). Saturation decreased after dusk in national parks but remained high for FSC-concessions. Similarly, we observed distinct diel cycles in closed forest during the dry season. The PCCA had a larger dusk peak compared to both logging types and exhibited an earlier and larger peak just before dawn. Both logging types had a later dawn peak but lacked a pronounced dusk peak. In the rainy season, we see much greater coherence among forest designations.

3.2. Hunting

Over the survey period, we detected 573 gunshots across 79 sites, with high variability between sites. Gunshots should not be treated as absolute counts as they may be detected by more than one detector within 4 km. No gunshots were detected in an additional twenty national park sites (Lopé and Moukalaba-Doudou) and ten FSC-certified logging sites. Collectively, non-certified concessions had the greatest gunshot rate, two times the daily gunshot rate of FSC-certified concessions and national parks (Table 1). The area of Ivindo National Park that we sampled had gunshot rates comparable to the non-certified

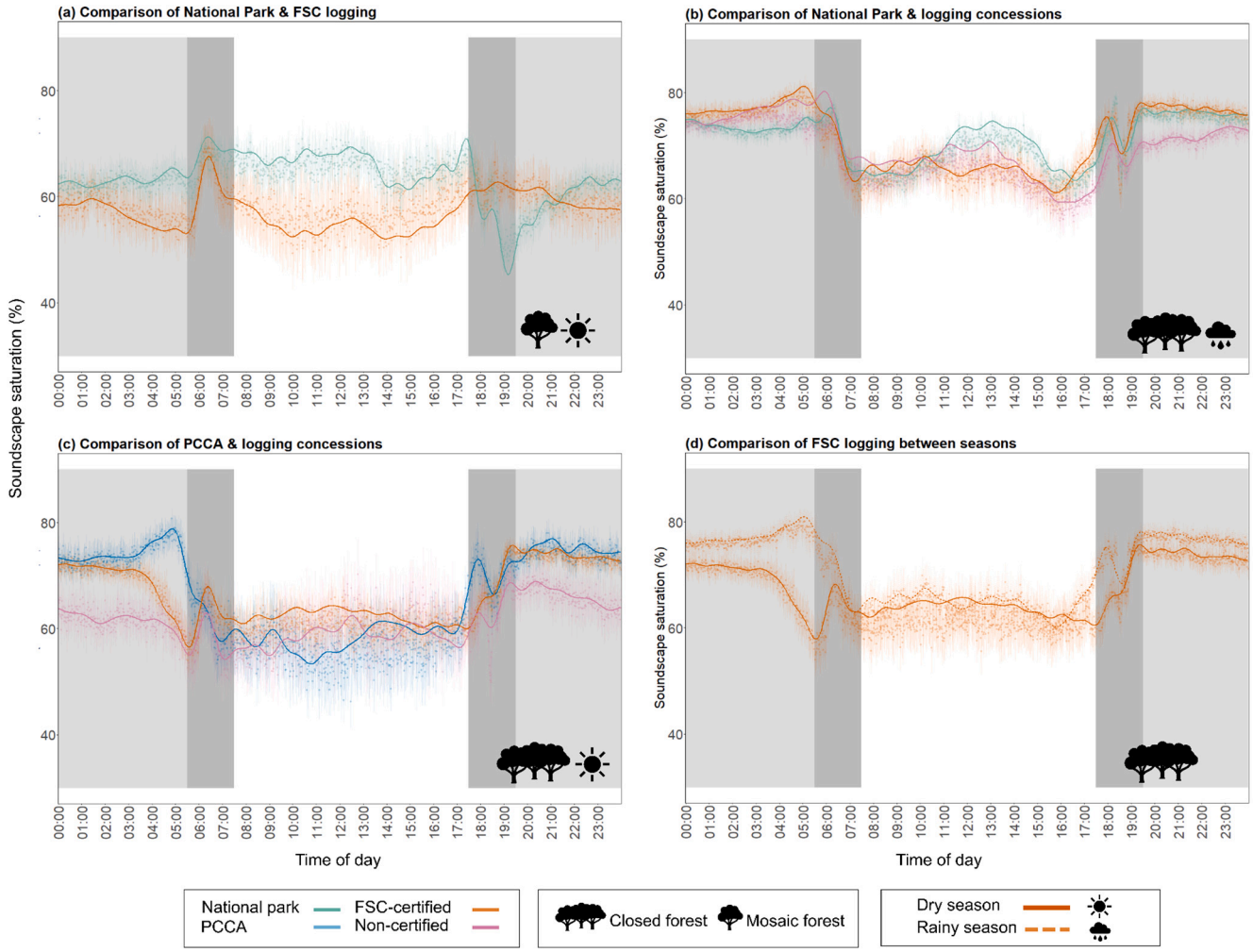


Fig. 3. Predicted soundscape saturation for (a) mosaic in the dry season, (b) forest in the rainy season, (c) forest in the dry season, and (d) forested FSC-certified logging concession sites. Points represent mean observed soundscape saturation per minute among forest designations with bars representing standard error. Light grey shading – night, dark grey shading – dawn and dusk. PCCA – proposed community conserved area.

concessions and the PCCA. We also identified seasonal differences in gun hunting that differed between forest types, with a 2.2-fold difference between the closed forest in the rainy season compared to the dry season (mean daily gunshot rate 1.20 and 0.54, respectively). However, hunting was higher in the dry season compared to the rainy season across mosaic sites (mean daily gunshot rate 0.18 and 0.02, respectively). The best performing model to predict responses to hunting included daily gunshot rate and forest designation. Higher gunshot rates were associated with lower saturation in both forest designations where sufficient variation existed, national parks and non-certified concessions (Fig. 4b). This relationship was highly non-linear (effective degrees of freedom = 7.98), with the rate of decline being greatest at the highest gunshot rates (Fig. S3, Table S5). Relative accessibility did not improve the model fit.

3.3. Time since logging

The best performing model to predict the impacts of logging on soundscape saturation included years since logging and forest designations (Table 2). Recently logged sites had lower saturation across much of the diel cycle compared to sites logged 20+ years prior (Fig. 4). This was the case in both types of logging concession. Canopy height and relative accessibility did not significantly improve model performance (Table S3).

Table 2
Top three models for predicting soundscape saturation in response to (i) logging, and (ii) hunting. Note that data differs between logging and hunting models. All models and model equations are available in Table S3. Equ. – Corresponding model equation (see Table S3 for all models); K – estimated number of parameters; ΔAICc – difference in Akaike Information Criterion corrected for small sample sizes.

Equ.	Top models	K	ΔAICc
Logging			
15	*Forest designation* + *Year since logging* + s(*Minute since midnight*, by = *Forest designation*, k = 50)	152	0
14	*Forest designation* + s(*Minute since midnight*, by = *Forest designation*, k = 50)	151	1491
11	*Year since logging* + s(*Canopy height*) + s(*Minute since midnight*, k = 50)	61	15,708
Hunting			
24	*Forest designation* + s(*Daily gunshot rate*) + s(*Minute since midnight*, by = *Forest designation*, k = 50)	160	0
19	(*Daily gunshot rate*) + s(*Minute since midnight*, by = *Daily gunshot rate rounded*, k = 50)	207	6590
20	*Forest designation* + s(*Minute since midnight*, by = *Forest designation*, k = 50)	151	10,603

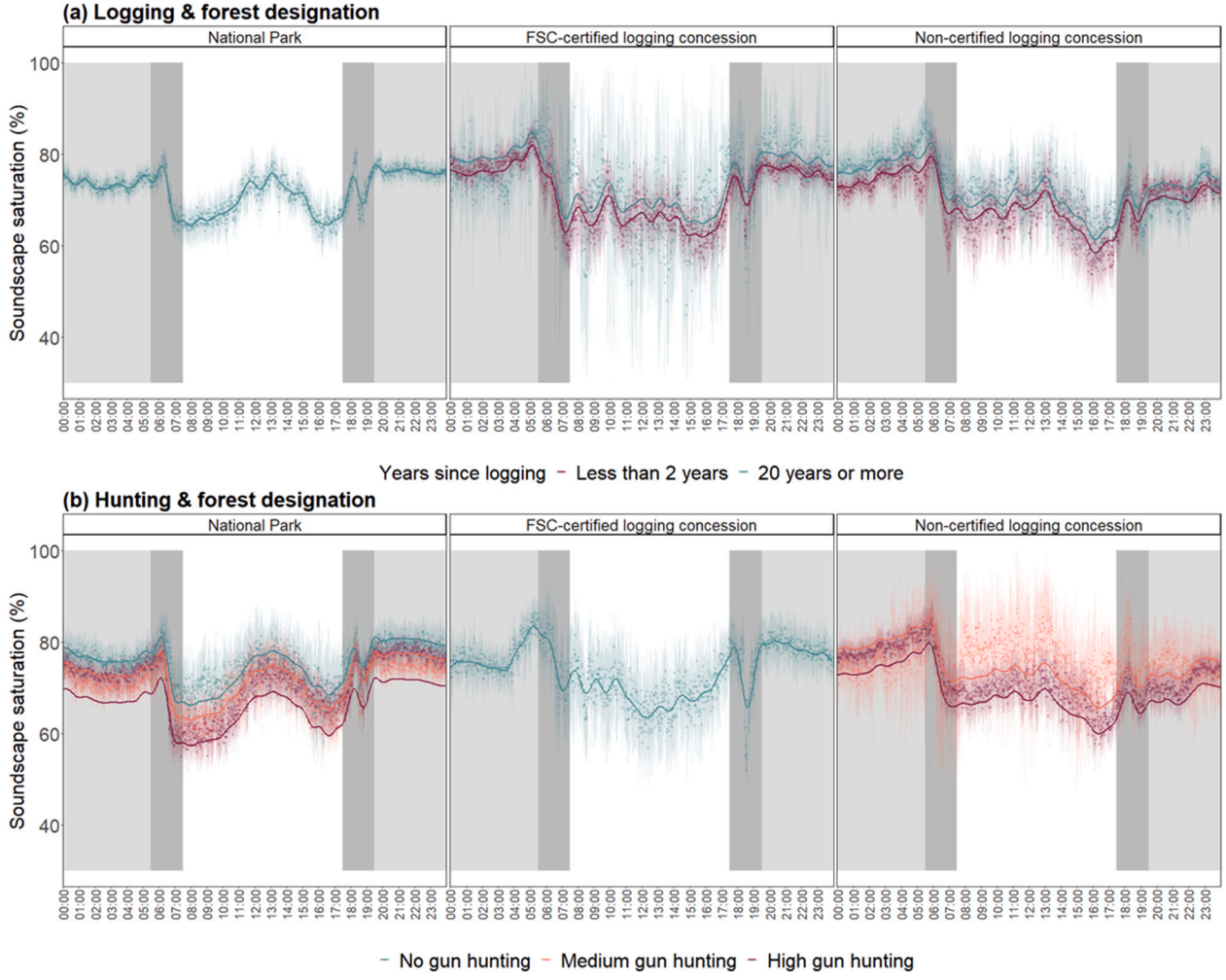


Fig. 4. Predicted soundscape saturation in relation to (a) logging and (b) hunting within each forest designation. Points represent mean observed soundscape saturation per minute among forest designations with bars representing standard error. Hunting pressure is represented by values for the 0 % (no gun hunting), 50 % (medium gun hunting), and 100 % (high gun hunting) quantiles of daily gunshot rate. The points representing mean gunshot rates have been rounded to these categories for the purposes of visualization. Forest designations represent forested sites in the rainy season. Light grey shading – night, dark grey shading – dawn and dusk.

3.4. Relationship between soundscape saturation, background noise, and sonotype richness

Across the sample of 92 independent minutes, we found 113 different sonotypes, comprising unique bird, mammal, amphibian, and insect sounds. Several endangered and critically endangered species were represented within these sonotypes, including the western lowland gorilla, the African grey parrot (*Psittacus erithacus*), and the chimpanzee (*Pan troglodytes*). There was a significant positive relationship between sonotype richness and overall soundscape saturation ($p = 0.001$, Fig. 5), although the explanatory power was low (adjusted $R^2 = 0.1$).

4. Discussion

In Central Africa, national parks and FSC-certified concessions are considered crucial for biodiversity conservation, particularly for many threatened species, such as great apes and elephants (Clark et al., 2009; Tchakoudeu Kehou et al., 2021; Zwerts et al., 2024), that are otherwise negatively impacted by deforestation, excessive timber extraction, and hunting (Imai et al., 2009; Lhoest et al., 2020; Sollmann et al., 2017). We found evidence that national parks and FSC-certified concessions in Gabon harbour a greater vocalizing diversity than non-certified concessions, likely in part due to greater hunting restrictions. We also found forest not logged for twenty to forty years had greater soundscape saturation compared to recently logged sites. However, the soundscapes of forests with any previous logging, even those logged 20+ years ago, were significantly different to the soundscapes from a limited number of sites that had never been logged. This change in the soundscape suggests logging activity has a lasting legacy on the soundscape. Our findings also suggest that FSC-certified concessions are effective at reducing gun hunting pressure compared to non-certified concessions.

4.1. Hunting

Our results show that designated land use classes do not necessarily correspond to hunting and logging pressures in a uniform and expected way. In Gabon, licenses can be obtained to hunt in buffer zones of national parks, community forests, and logging concessions, but hunting is prohibited in national parks (The Forest Code, 2007). Despite this, we found national parks with both high and low hunting rates (1.12 and 0.02 mean gun daily gunshots in Ivindo NP and Lopé NP respectively). This variation likely reflects the relative accessibility at the sites rather than different levels of law enforcement or management, as all parks are managed by Agence Nationale des Parcs Nationaux (Lhoest et al., 2020; Poulsen et al., 2017). Personnel in all three parks reported being understaffed to engage with local communities at a meaningful level and to enforce hunting laws (pers. obs.). We sampled a relatively accessible area of the Ivindo NP, which can be reached by boat from the Ivindo River or by vehicle from a national road leading to the provincial capital. Hunting decreases towards the core area of Ivindo NP. Overall, we observed lower gun hunting rates in FSC-certified concessions compared to non-certified concessions, and in some cases, compared to national parks. Certified concessions often have greater on-the-ground presence and resources to enforce hunting restrictions than national parks (Harrison, 2011). In this way, certified concessions have been shown to protect wildlife from illegal hunting in Central Africa through active management strategies - at least while operating (Clark et al., 2009; Zwerts et al., 2024).

Widespread, uniform hunting bans have been criticized as many consumers lack access to reliable, affordable, and safe alternative food or sources of income (Wilkie et al., 2016). Logging concessions may increase employment opportunities and provide better infrastructure to connect small settlements to larger urban areas (e.g., Hymas, 2016; Lescuyer et al., 2012). However, such infrastructure development can present a double-edged sword. Logging infrastructure also enables greater accessibility to remote areas, increasing demand for goods including wild meat, which can lead to the overexploitation of forest resources and reduce food and income security for local people (Hymas, 2016; Poulsen et al., 2009). Unless management practices like road closures are implemented, then logging infrastructure may ultimately lead to greater forest loss and hunting pressure, even beyond the lifespan of the concession (Buřivalová et al., 2020; Kleinschroth and Healey,

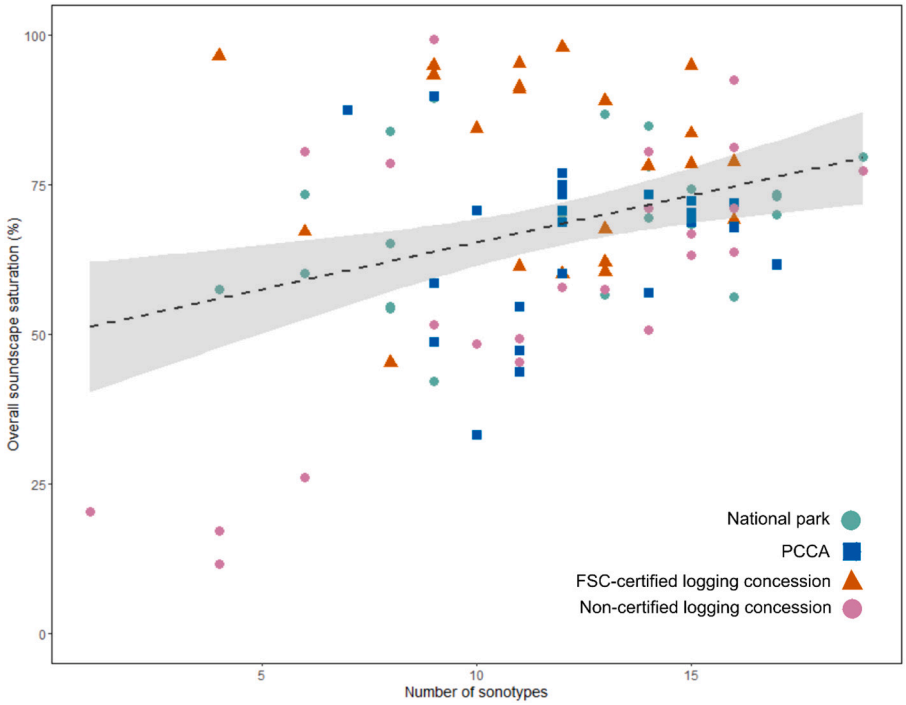


Fig. 5. Relationship between the number of sonotypes and overall soundscape saturation ($p = 0.001$, adjusted $R^2 = 0.097$). Each point represents one site per minute and the grey shading represents 95 % confidence intervals. PCCA – proposed community conserved area.

2017; Poulsen et al., 2009). It is beyond the scope of this work to make recommendations for hunting management, but our study underscores the importance of measuring hunting pressure, rather than making assumptions according to land use categories (see Froese et al., 2022 for more).

In Gabon, a broad range of taxonomic groups are hunted but ten species can represent 50 % of offtake, most of which are diurnal mammals (Froese et al., 2023). We found greater gun hunting was associated with lower soundscape saturation in logging concessions. It is unlikely this decline is driven by the direct impacts of hunting given many of the most commonly hunted species (e.g. duiker, porcupine, pangolin) are not highly vocal and therefore are poorly sampled using acoustic monitoring. However, it is worth noting that alternative hunting methods, such as traps, are less discriminate. The decline observed more likely reflects indirect impacts of hunting on the forest community. Overhunting in Central Africa, particularly of large, frugivorous mammals, is known to disrupt the ecological functioning of tropical forests, leading to changes in forest structure, seed dispersal, and species diversity (Abernethy et al., 2013). These changes in turn can have cascading consequences for other species groups more readily detected using acoustics, e.g. phytophagous insects (Peguero et al., 2017). Alternatively, the relationship between soundscape saturation and gun hunting may be capturing another component of disturbance not otherwise represented in our study.

4.2. Logging

Forest designation was not an informative predictor of logging impact, mostly due to historical factors rather than expansive illegal logging. For example, most national parks had been established partially in retired logging concessions, last logged 20 to 40 years prior to our study. Meanwhile, the proposed community conserved area (Ibola Dja Bana Ba Massaha) included sites within a non-certified concession that had not been industrially logged in known history. The never logged sites had a greater soundscape saturation compared to comparable logged sites during dawn and dusk (Fig. 3). Previous meta-analyses found that some bird species do not recover their populations even ~40 years after logging (Buřivalová et al., 2015), and the role of habitat legacies (e.g., large, hollow trees being more abundant in never logged forests) is well documented (Meijaard et al., 2005). As such, even decades-old logging activity may contribute to lasting changes in soundscape saturation and old-growth forests are considered irreplaceable (Gibson et al., 2011). In light of this, we recommend not logging in previously unlogged areas (Barlow et al., 2010; Edwards et al., 2019; Gibson et al., 2011).

During our study, the legal status and designation of Ibola Dja Bana Ba Massaha was under review following a request from the Kota community of Massaha to the Gabonese government, requesting logging rights be retracted due to the forest's biocultural value. If this request is granted, the area will become Gabon's first community conserved area. This community conserved area would differ from the community forestry sites already managed by the Massaha community as it would represent forest managed for purposes other than timber extraction. Note that since the conclusion of our data collection, three of the five never logged sites we describe here have been selectively logged.

Even though biodiversity is likely to remain altered for 40+ years, we did find signs of recovery - soundscape saturation was higher in forests twenty to forty years post-logging compared to forests that have been recently logged. The economic importance of timber extraction for many countries including Gabon is clear (ITTO, 2022) and it is less environmentally detrimental than complete deforestation for large-scale agriculture or plantations (Gibson et al., 2011). As we show, FSC-certified logging can be as good as, if not better than, national parks at regulating hunting in Gabon. The additional difference in soundscape saturation between FSC and non-certified logging (beyond hunting) could be due to differing logging practices (Ezzine de Blas and Ruiz Pérez, 2008; Putz et al., 2008; Umunay et al., 2019), including the observation that certified loggers took greater care not to damage streams in at least two of the FSC-certified concessions (pers. obs.).

4.3. Diel and seasonal differences

Despite seasonal differences in the diel cycle, soundscape saturation decreased following dusk in non-certified concessions in both seasons. From ad hoc listening and the literature, we found that insect vocalizations dominate the overall soundscape (Aide et al., 2017). Monitoring tools that exclusively focus on megafauna, e.g. camera traps, risk overlooking how disturbance impacts the majority of animal species in tropical forests. Insect groups most represented in bioacoustic data include Orthoptera and cicadas, otherwise referred to as 'singing insects' (Ganchev et al., 2007). Orthoptera are considered highly sensitive to disturbance and are effective bioindicator species of disturbance in tropical forests (Riede, 1998). For example, in Southern Brazil, species of the family Gryllidae occur exclusively in open habitats, whereas Phalangopsidae are associated with forests with little disturbance (Szinwelski et al., 2012). Previous studies have shown that logging disturbance can affect litter depth, canopy height, and rates of deadwood, all of which influence invertebrate abundance and richness (Cole et al., 2016; Szinwelski et al., 2012) and moderate rates of logging have been linked to significant declines in insect abundance in Afrotropical forests (Opito et al., 2023). Therefore, future research should consider other structural and landscape metrics to examine additional impacts of logging (see Dupuis et al., 2023 for alternative data availability). Such studies should aim to quantify disturbance at smaller spatial scales to account for how logging may impact ecological communities at smaller spatial scales.

Beyond insects, the dawn and diurnal soundscapes were largely dominated by bird species, whereas nocturnal soundscapes consisted predominantly of vocalizing nocturnal anurans (frogs and toads) early in the night, and mammals, including tree hyraxes (*Dendrohyrax* spp.) and prosimian primates (e.g., Galagidae spp.) throughout the later part of the night (Channing and Rödel, 2019; Pijanowski et al., 2011; Rosti et al., 2020) – most of which are not hunted. Therefore, declines in vertebrate richness likely reflected declines in anuran and mammal richness in non-certified concessions, but suggests little change to diurnal bird activity. Such findings would be consistent with a meta-analysis by Buřivalová et al. (2014) which found mammal, amphibian, and invertebrate richness declines with increased selective logging intensity, in contrast to bird richness which increases due to an influx in habitat generalists. Therefore, it is important to recognize that metrics such as soundscape saturation do not capture the replacement of forest specialists with generalists. Targeted research in the future could investigate how individual species are impacted by the indirect effects of hunting or differences in microhabitats among forest designations. Similar to Zwerts et al. (2022), we observed substantially different soundscapes between closed rainforest and mosaic forest. This likely reflects differences in the animal communities between the two habitat types. Forest mosaics provide more open habitat, less well-suited for many nocturnal forest species (Tutin et al., 1997). This may explain the low saturation we observed at night in the mosaic forest for both national parks and FSC-certified logging. Our results highlight the importance of comparing "like-with-like" in soundscape studies.

4.4. Limitations and future research

Although soundscape saturation can be used as a broad indicator of vocalizing diversity, it cannot be used to understand species-specific responses to disturbance. Using soundscape saturation in combination with species recognition tools (e.g., BirdNET; Kahl et al., 2021) can provide a more comprehensive approach for monitoring vocalizing species. We used individual sound recognition to focus on measuring gunshot sound but we encourage future work to explore our dataset for

individual species (see Data Availability Statement). Unlike in Latin America and Asia, bioacoustics is not yet widely used for conservation in Central Africa, partially due to the lack of reference data for many species (Becker et al., 2022). Similarly, there is a lack of accessible reference data for invertebrate calls, including well-detected taxa such as Orthoptera (Riede, 2018), which hinders monitoring efforts.

For less vocal species, such as duikers, camera trap studies better capture responses to hunting and logging (for example see Nuñez et al., 2019; O'Brien et al., 2020; Simo et al., 2023). While gunshot detection provides a useful metric for hunting across the landscape, we note that many gunshots were detected simultaneously by multiple detectors within a forest unit (e.g., between two adjacent sites), resulting in spatial autocorrelation. Therefore, these findings should not be treated as a score of absolute hunting but rather as a relative comparison of hunting rates among forest designations. Our accessibility layer provides one way to try to capture other forms of hunting across a large area. Alternatively, distance to the nearest village can provide a simple metric to predict hunting pressure (Beirne et al., 2019). However, neither approach accounts for differences in enforcement, hunter preference, or other factors influencing hunter movement across the landscape. Engaging with local hunters to determine hunting trails and offtake would provide a more accurate reflection of hunting pressure, e.g. Froese et al. (2022). It is also important to consider that geophony may artificially inflate soundscape saturation as this index is not designed to remove instances of rain (Sánchez-Giraldo et al., 2020). Although tools such as the R package hardRain (Metcalf et al., 2020) can isolate rain from soundscape recordings, such analysis remains difficult to perform on continuous acoustic datasets due to processing and data storage demands. We echo calls for more research into how geophony may influence research findings in soundscape studies (Sánchez-Giraldo et al., 2020) and encourage future research to investigate seasonality further.

5. Conclusions

We conclude that FSC-certified forestry appears to maintain greater vocalizing diversity compared to non-certified logging, likely mostly due to lower rates of hunting. National parks can play an important role in preserving inaccessible areas and preventing further logging. However, without additional interventions, accessible areas of national parks can have high rates of hunting, similar to non-certified logging concessions. We demonstrate that sites that had been logged several decades prior have higher vocalizing diversity than recently logged sites. Yet even sites that had been logged decades ago still differ substantially from never logged forest, which are becoming increasingly rare. We therefore advocate for the few remaining never logged forests to be urgently withdrawn from the selective logging estate in Gabon. In conclusion, safeguarding forests that had never been logged before - be it within traditional top-down or new bottom-up protected areas - while increasing the proportion of FSC-certified logging concessions, can effectively bolster forest conservation in Gabon and throughout the Congo Basin.

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CRediT authorship contribution statement

Natalie Yoh: Writing – original draft, Visualization, Formal analysis, Data curation. **Walter Mbamy:** Project administration, Investigation, Conceptualization. **Benjamin L. Gottesman:** Formal analysis, Conceptualization. **Graden Z.L. Froese:** Writing – review & editing, Project administration, Investigation, Conceptualization. **Tatiana Satchivi:** Project administration, Methodology, Investigation. **Médard Obiang Ebanega:** Project administration, Investigation, Conceptualization. **Lauren Carlson:** Investigation. **Serge Ekamza Koto:** Project administration, Investigation. **Mutlu Özdoğan:** Resources. **Dave J.I. Seaman:** Formal analysis. **Vincent Maicher:** Project administration, Investigation. **Halina Malinowski:** Project administration, Investigation. **John Poulsen:** Project administration, Funding acquisition. **Alex Ebang Mbélé:** Project administration, Investigation. **Zuzana Buřivalová:** Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

This work has been partially funded by the Precious Forest Foundation which is connected with the tropical forest logging industry, including in Gabon. Neither the Foundation nor any representatives of the industry provided input or influenced through any pressure the outcomes of the analyses or the interpretation of the results. Additionally, several co-authors are involved in and advocate for the establishment of the Proposed Community Conserved Area described in this study. Overall, the positionality of most co-authors can be expressed as invested in biodiversity conservation, sustainable development, and local communities' rights.

Data availability

Data is to be made available from the Dryad Digital Repository upon manuscript acceptance. Data & code for the koogu model is available at https://zenodo.org/records/11192704

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110726.

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