Assessing the structure and drivers of biological sounds along a disturbance gradient

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ABSTRACT

Studying soundscapes to improve knowledge about an environment with limited visibility is gaining popularity. However, the structure and drivers of biological sounds remain poorly understood although this information can improve understanding of landscape dynamics. To describe biological sounds and provide a better understanding of their drivers, we conducted a study aiming at detecting and identifying individual vocalising animal species, determining the abundance, diversity, and composition of vocalisations, and assessing how ecological and anthropogenic factors affect these sounds. Sounds were recorded from February through May 2020 in southeast Cameroon, using passive acoustic monitoring, in three study sites representing a gradient of disturbance. Local experts listened to 20,485 1-min files of recorded sounds to identify vocalising species. These identifications, in combination with anthropogenic and ecological data from the field, were used to assess abundance, diversity, and composition of vocalisations. Fifteen vocalising mammal species and 37 vocalising bird species were identified. Overall, insects and, to a lesser extent, birds were the most dominant animal classes in the soundscape. Furthermore, vocalisation abundance and the diversity of vocalising mammals did not vary along the disturbance gradient, whereas vocalisation abundance of birds was lowest in the site where anthropogenic disturbance was least present. Moreover, both mammal and bird vocal activity were negatively impacted by rainfall. Human activity and the amount of swamp habitat reduced the vocal activity of mammals, but these factors did not affect bird vocalisations. For birds, the diversity of vocalisations was positively affected by bird abundance and negatively affected by higher temperatures. Our results indicate that animal classes do not have the same number of acoustically active species and produce differing amounts of sound, thus highlighting that sources of sound do not make equal contributions to the soundscape and furthering knowledge of soundscape structure. They also show that the effects of anthropogenic and ecological factors on biological sounds vary depending on the sound source, which suggests that soundscape components are differently affected by soundscape drivers. Additionally, our study provides baseline acoustic information on vocalising species in African tropical rainforests. This acoustic information may be used for automated detections of vocalisations in the future. Together, an understanding of soundscape drivers and information on vocalising species can contribute to the development of applications that will monitor soundscapes and detect important

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changes in landscapes. This will help guide future decision making and landscape conservation planning.

1. Introduction

A soundscape or acoustic community, defined as the assembly of all sounds emitted from a landscape, comprises sounds of animals (biological sounds), sounds from nonbiological sources (geophysical sounds), and human or anthropogenic sounds (Pijanowski et al., 2011a). The structure of a soundscape shows spatial and temporal variability and reflects important anthropogenic and ecological processes (Pijanowski et al., 2011b; Sueur et al., 2014; Sueur and Farina, 2015). The soundscape is shaped by factors such as human activities, biophysical characteristics, animal community, and climate (Pijanowski et al., 2011a; Sethi et al., 2020). Additionally, soundscape patterns can vary depending on the time of day and the season (Depraetere et al., 2012; Haver et al., 2020).

Research on soundscapes has gained popularity in recent years (Browning et al., 2017; Deichmann et al., 2018; Sugai et al., 2019). Many studies have investigated soundscapes based on acoustic indices, which are mathematical functions that describe some aspect of the complexity or diversity of sound recordings (Browning et al., 2017; Ferreira et al., 2018; Borker et al., 2019). Unfortunately, studies that monitor biological sounds (also known as biophony; Krause [1987]) using acoustic indices are often limited and biased due to sensitivity to background noise from rain, wind, or anthropogenic sounds (Farina et al., 2011; Fairbrass et al., 2017). In addition, studies based on these indices do not allow for the identification of individual vocalising species or their contribution to the soundscape (Browning et al., 2017). So far, studies of biological sounds were mainly limited to ornithology (Farina et al., 2011; Tucker et al., 2014; Gasc et al., 2017; Borker et al., 2019; Teixeira et al., 2019). However, there is a need to focus on the contribution of other taxonomic groups to the soundscape as well (Ferreira et al., 2018). Furthermore, the use of soundscape monitoring to reveal ecosystem disturbances was rarely considered (Gasc et al., 2017). Studies that assessed the impact of potential factors driving biological sounds mainly focussed on anthropogenic noise, seasonality, and time of day (Depraetere et al., 2012; Fuller et al., 2015; Shannon et al., 2016; Haver et al., 2020). However, the effect of other anthropogenic and ecological factors on biological sounds remains poorly understood (Lomolino et al., 2015; Sueur and Farina, 2015; Eldridge et al., 2016).

Studies of biological sounds involving the identification of vocalising species may help to uncover new insights regarding the composition of vocalising animal communities and contribute information necessary for more precise estimates of soundscape components. In addition, studying biological sounds to identify individual vocalising species is the first step towards the demanded development of classifiers required to improve existing call libraries and facilitate automatic identification of species in future soundscape studies (Browning et al., 2017; Gasc et al., 2017). Assessing how the abundance, diversity, and composition of vocalisations varies in relation to a wide suite of anthropogenic and ecological covariates can provide a clear overview of the factors affecting the dynamics of biological sounds. These insights may shed light on the understanding of soundscape drivers (Pijanowski et al., 2011a).

Our study aims to detect and identify vocalising species, determine the structure of biological sounds (abundance, diversity, and composition of vocalisations), and evaluate the effects of anthropogenic and ecological factors on biological sounds. Here, anthropogenic variables such as human activity and distance to trails and villages are used as a proxy for disturbance. Ecological factors include habitat, animal community structure (animal abundance, diversity, and composition) and weather conditions. Vocalising animals from multiple taxonomic classes are considered. However, only mammals and birds are used to evaluate the impact of these factors on vocalisation patterns because species from these animal classes are relatively easy to identify. We address the following three research questions: Do animal classes contribute equally to the soundscape? Does the structure of biological sounds vary along a disturbance gradient? How do anthropogenic and ecological factors drive biological sounds? Animals widely differ in their frequencies for sound communication (Fletcher, 2004). Therefore, the level at which different animal classes contribute to the soundscape is expected to vary. Anthropogenic noise, which is a form of disturbance, affects the vocal behaviour of wild animal species (Shannon et al., 2016). Hence, the structure of biological sounds is expected to vary along a gradient of anthropogenic disturbance. Furthermore, anthropogenic disturbance alters animal community structure (Tagg et al., 2011, 2015; Laméris et al., 2020). This alteration is expected to translate to changes in vocalisation patterns and, therefore, modifications of biological sounds (Kalan et al., 2015). Animal behaviour is influenced by the immediate physical setting where animals live, and seasonality is known to drive vocalisations (Wong and Candolin, 2015; Haver et al., 2020). Therefore, habitat and weather conditions are also predicted to affect animal vocal behaviour and, thus, biological sounds.

Table 1
Overview of how the three study sites represent a disturbance gradient.

| Site	Population size (#)	Land-use type	Conservation management	Disturbance
Ngouleminanga	130	Community forest	Absent	High
La Palestine	176	Community forest	Present	Medium
La Belgique	182	Forest management unit	Present	Low

2. Methods

2.1. Study area

This study was conducted in the northern part of the Dja Faunal Reserve's buffer zone in Cameroon. Data were collected in three study sites (Ngouleminanga, La Palestine, and La Belgique) that differ in land-use type and conservation management (Table 1; Fig. 1). Information about the three sites was obtained from S. Dekegel (Unpublished results). Since the overall level of disturbance in a site depends on these two factors, these three sites are expected to represent a gradient of disturbance.

2.2. Data collection

Field work was conducted between February and May 2020, at the start of the wet season. During this time, bioacoustics measurements were performed for the detection and identification of individual vocalising species and the determination of biological sounds. A total of 18 AudioMoth bioacoustics sensors were deployed throughout the study area (6 per site). In each site, six transects of 1 km each were opened and one sensor was deployed in the middle of every transect, at the 500-m mark (Hill et al., 2019). To create enough space between the transects within each site, a cascading design was used.

All sensors were set to record the first minute of every hour, resulting in 24 min of sound recordings per transect per day. In total, 20,485 min of sound were obtained from the three sites. This corresponds to 5949, 7712, and 6824 recorded minutes in Ngouleminanga, La Palestine, and La Belgique, respectively. Additionally, 1895 audio files were discarded because they were recorded during periods of rain which caused background noise. To expedite the listening process, all recordings made during the night were screened beforehand. Only night recordings that contained vocalisations other than those of insects, amphibians, or western tree hyraxes (*Dendrohyrax dorsalis*), which were all easily recognisable after some training, were played to the local expert listeners for identification. All remaining recordings were played to two local villagers who could identify the audible species. For each recording, these local experts were asked to write down the names of all the species they heard in their local language, Badjué. The English and scientific translation of many of the local names were already known; if not, the local experts were asked to pinpoint the species by referring to local identification guides (Borrow and Demey, 2002; Languy, 2019). When the local experts did not unanimously agree on the identification of an audible species, they were asked to reach a consensus through discussion or replaying a recording as many times as necessary. Since this study used mammals and birds to evaluate the impact of ecological and anthropogenic factors on
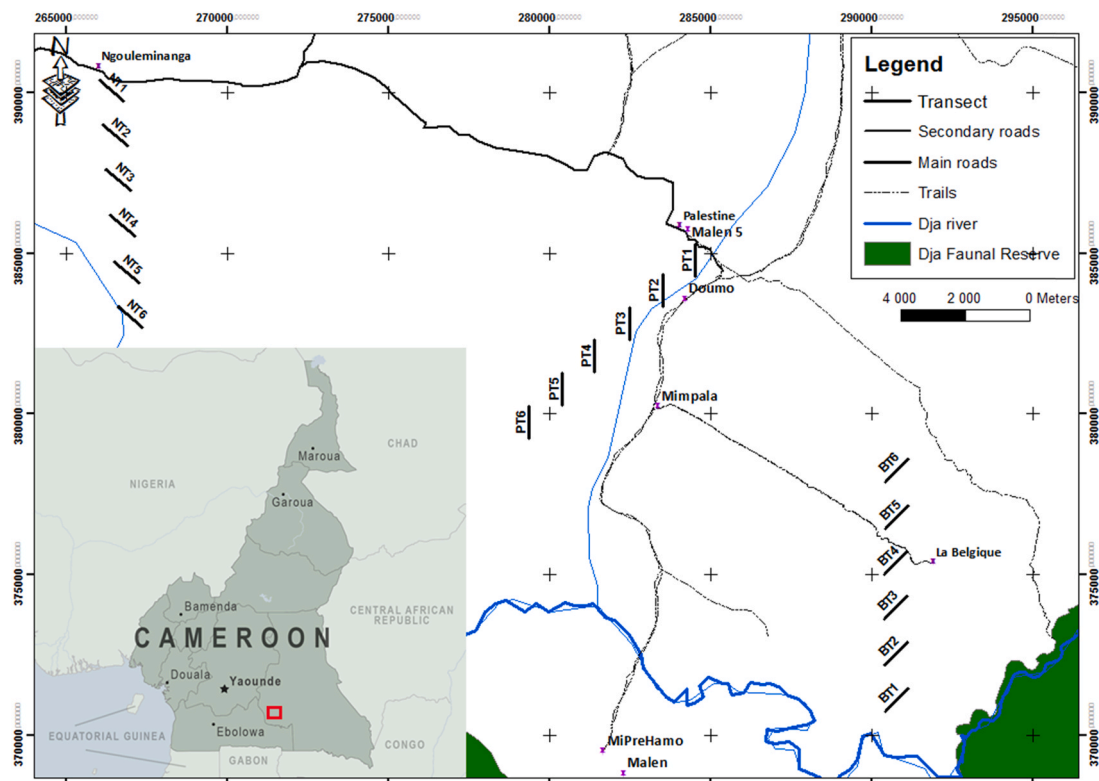
Fig. 1. Location of the three study sites and the adjacent villages in the northern periphery of the Dja Faunal Reserve in southeast Cameroon. Six 1-km transects were opened in each site using a cascading design. The transects were cut with a constant compass bearing of 140°, 180°, and 45° in Ngouleminanga, La Palestine, and La Belgique, respectively.

vocalisation patterns, vocalisations from these taxa were identified by species. Vocalisations from amphibians and insects were identified by class.

To assess the contribution of different animal classes to the soundscape, vocalisation abundance was determined for each vocalising animal. All 1-min recordings (from all transects) were pulled together. The number of recordings in which an animal class was present was divided by the total number of recordings in order to obtain the vocalisation rate for each class.

To assess how biological sounds vary among sites with differing levels of disturbance, abundance and diversity of vocalisations were compared across study sites. For vocalisation abundance, differences in vocalisation rates per sensor per day across study sites were evaluated for each species. To ensure reliable analysis, only data recorded in all sites on the same day, at the same time, and by a set of sensors with similar spatial designs were used. To compare diversity of vocalising species across sites, sound recordings were only used from times in which all acoustic sensors in all three study sites had made recordings without background noise. For each vocalising species, the number of sound recordings in which the species was present was determined per site. With these numbers, rarefaction curves were plotted with iNEXT (Chao et al., 2016). These curves were extrapolated to larger sample sizes to estimate asymptotic species richness and compare diversity across sites.

To assess the drivers of biological sounds, data on anthropogenic and ecological factors were collected during field surveys. In each transect, habitat description and surveys of human activities, mammals (both direct and indirect observations), great apes, and birds were conducted. During the surveys, a researcher walked along the transect accompanied by one or more local guides who were able to detect and identify signs. Additionally, data on precipitation (mm), temperature (°C), and humidity (%) were obtained per day. To assess differences between study sites based on data obtained during field surveys, the encounter rate (observations/km) was used. Thus, for every transect, the mean number of observations for each type of field survey data was calculated. To investigate the influence of the habitat structure, the total length of swamps and terra firma forests (mature forest, old secondary forest, young secondary forest, and light gaps together) in the transects was calculated (Willie et al., 2013). Thereafter, the total amount of human, mammal, and bird signs in swamps and terra firma forests was determined. Human activity was calculated overall and broken down into hunting signs and other human signs. The encounter rates of mammal and bird signs were used as an index of species abundance. To evaluate additional anthropogenic factors that might affect biological sounds, ArcGIS was used to measure the shortest straight-line distance(m) between the sound recorders and the closest village and trail. The distance between the recorder and the closest village served as a proxy for the remoteness of the recording location, whereas distance between the recorder and the nearest trail was used as a measure of accessibility.

To assess how anthropogenic and ecological factors affect biological sounds, obtained values of mammal abundance, bird abundance, human activity, geographical factors, and climatic measurements were used as predictor variables. Furthermore, two dependent variables were calculated. Since we did not have the same number of recordings for each site, these variables were calculated per sensor per day. The first dependent variable is the proportion of files that contained vocal activity. This proportion, used as a proxy for abundance of vocalisations, was calculated by dividing the number of recordings with vocal activity by the total number of recordings per sensor per day. The second dependent variable is the number of species identified per sensor per day. This variable was used as a proxy for bioacoustic diversity. These dependent variables were calculated for all bird species together and all mammal species together. Data obtained during field surveys on transects were attributed to the corresponding sensors. Additionally, the percentage of swamp and terra firma forest was calculated per transect, thus per sensor. Note that only observations of dependent variables for which values for all predictor variables were available were used. This resulted in a total of 847 observations.

2.3. Statistical analysis

To determine the structure of biological sounds, normality of all processed data, obtained during the identification of sound recordings, was tested per study site using the Shapiro-Wilk's test. Normally distributed data were tested for homogeneity of variances using a Bartlett test. If data for one of the compared study sites followed a non-normal distribution, a Kruskal-Wallis one-way analysis of variance test was always used because this test does not assume equal variances. As post-hoc analysis, to determine which study sites differ significantly, Dunn's multiple comparison test with Benjamini-Hochberg correction was performed (Ogle et al., 2017). If data for all study sites were normally distributed and showed equal variances, a one-way ANOVA test was used with Tukey Honest Significant Differences post-hoc analysis. For normally distributed data with unequal variances between study sites, a Welch ANOVA test with Games-Howell post-hoc analysis was performed.

The sound data in this study were collected using a hierarchical design, where the moment of recording is nested in transects, which are nested in different study sites. However, preliminary multi-level analyses did not result in a need to treat data from different sites and times differently when assessing the drivers of biological sounds. Therefore, to evaluate the effect of anthropogenic and ecological factors on biological sounds, generalised estimating equations (GEE) were used. GEE are an extension of generalised linear models that allow for the analysis of repeated measurements where observations in separate clusters are independent (Halekoh et al., 2006). To assess multicollinearity among predictor variables, the variance inflation factor (VIF) of each variable was calculated. Variables with VIF > 5 were excluded from the analyses (O'Brien, 2007). Additionally, correlation analyses for all pairs of quantitative variables were run. Only temperature and humidity were strongly correlated. Since temperature was measured with more precision, humidity was excluded from the analyses. Poisson models for all dependent variables were used to assess dispersion. Since the number of recordings per sensor per day was not always equal, an offset variable (calculated as log of the total amount of recordings per sensor per day) was added to the models. Models with a dispersion statistic of $0.8 < \sigma_p < 1.2$ were considered normally dispersed (Payne et al., 2018). Bioacoustic diversity of all wildlife together and birds separately was normally dispersed, whereas total abundance of vocalisations and bird vocalisation abundance was underdispersed. Mammal bioacoustic diversity was also underdispersed, and mammal vocalisation

abundance was overdispersed. For models that showed under- and overdispersion, binomial GEE analyses were run without an offset variable. However, binomial GEE models require the dependent variable to be a proportion, but mammal bioacoustic diversity was represented as a count value. Therefore, these values were divided by the total number of vocalising mammal species identified throughout the study period to obtain a proportion of bioacoustic diversity. For the GEE analyses, the "exchangeable" correlation structure was used, and waves were added to maintain the chronological order of the repeated measurements. The fitted GEE models were compared to similar models to which weights were added to account for the different numbers of recordings that were available per sensor per day. The models were compared using the QIC program to select the GEE model that best fits the dataset (Cui, 2007). Models without weights proved to fit the dataset better. Therefore, results from these models were saved.

For a detailed site and method description, refer to MethodsX article by Diepstraten et al. (2021): Methods to measure biological sounds and assess their drivers in a tropical forest.

3. Results

In total, 52 different species were identified from the analysed sound recordings (Table 2 Supplementary Information). This total consisted of 15 vocalising mammals and 37 vocalising birds. Amphibian and insect vocalisations were detected in every site, but the local experts were unable to name the exact species based on sound alone.

To compare vocalisation rates across animal classes, 18,590 1-min recorded audio files were used. Bird vocalisations were present in $57.88\% \pm 1.46\%$ of the recordings. Second, mammal vocalisations were present in $9.34\% \pm 0.48\%$ of the recordings. Likewise, amphibian vocalisations were present in $8.31\% \pm 0.20\%$ of the recordings. Finally, insect vocalisations were present in every $(100\% \pm 0\%)$ recording. Therefore, the vocalisation rate of insects was significantly higher than that of birds, mammals, and amphibians (Dunn's Multiple Comparison test: $Z = 2.60, 6.10$, and 6.90, respectively; $p = 0.01, 3.18e-09$, and $3.06e-11$, respectively; Fig. 2). In addition, bird vocalisations were detected significantly more frequently than vocalisations of mammals and amphibians (Dunn's Multiple Comparison test: $Z = 3.50$ and 4.30, respectively; $p = 6.99e-04$ and $3.88e-05$, respectively; Fig. 2). There was no significant difference between mammal and amphibian vocalisation rates (Dunn's Multiple Comparison test: $Z = 0.80, p = 0.42$).
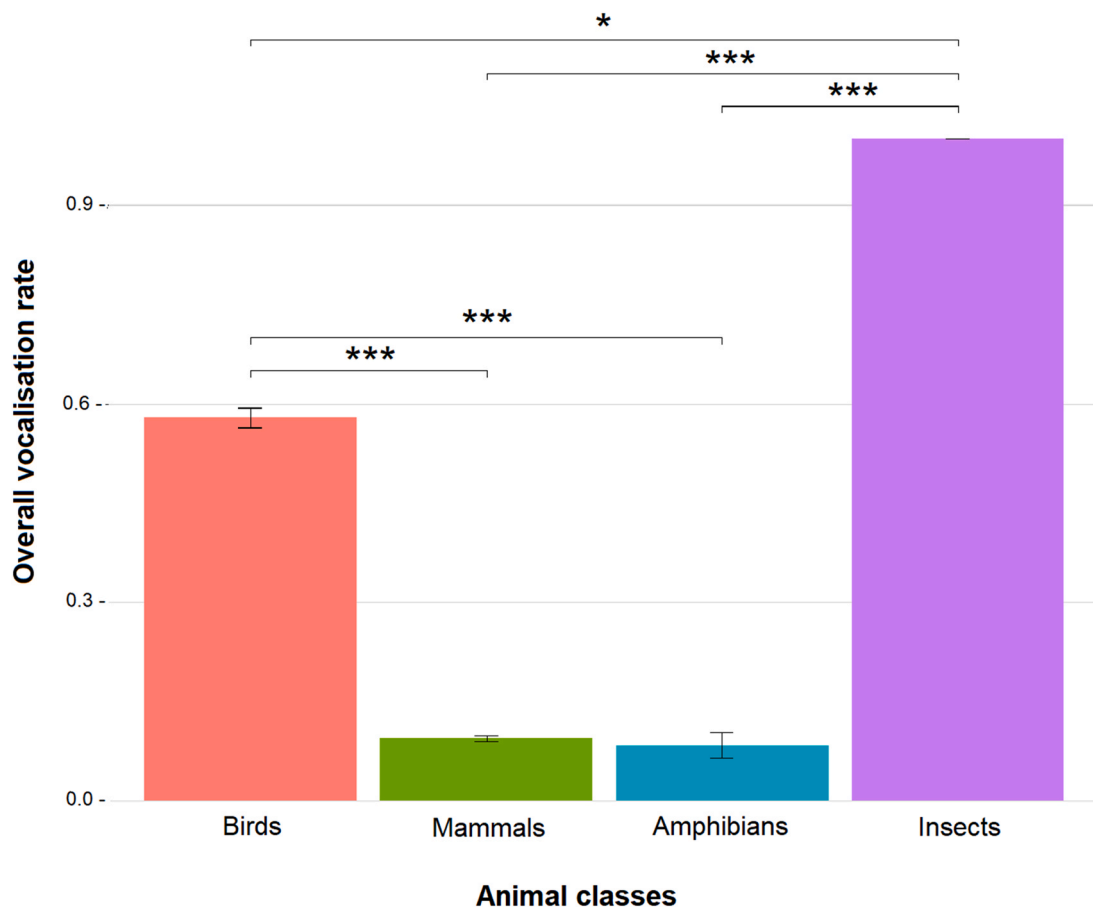
Fig. 2. Overall differences in vocalisation rates across animal classes based on data from all audio files. Standard errors are represented by error bars. Asterisks show significant differences (*: $p = 0.05$, **: $p = 0.01$, ***: $p = 0.001$).

After calculating vocalisation rates for all vocalising species combined, the lowest total rate was found in La Belgique with 18.50 ± 0.77 vocalisations per sensor per day. This was significantly less compared to both La Palestine and Ngouleminanga, with a total of 21.00 ± 0.86 and 22.30 ± 0.52 vocalisations per sensor per day, respectively (Dunn's Multiple Comparison test: $Z = -2.44$ and -4.00, respectively; $p = 0.02$ and 0.0002, respectively). Concerning vocalising mammals, all mammal species combined showed a vocalisation rate of 0.71 ± 0.11 in La Belgique, 0.77 ± 0.10 in La Palestine, and 0.62 ± 0.11 in Ngouleminanga. These differences were not significant ($p = 0.39$). However, the majority of recorded vocalisations were produced by bird species. All bird species combined had a vocalisation rate of 17.81 ± 0.76 in La Belgique, 20.19 ± 0.86 in La Palestine, and 21.73 ± 0.53 in Ngouleminanga. Similar to the total vocalisation rate, bird vocalisation rates in La Belgique were significantly lower than in La Palestine (Dunn's Multiple Comparison test: $Z = -2.34$, $p = 0.030$) and Ngouleminanga (Dunn's Multiple Comparison test: $Z = -4.10$, $p = 0.0001$). Vocalisation rates for all identified species are presented in Table 3 of the SI.

To compare vocalisation diversity along a disturbance gradient, Fig. 3 displays the interpolated (rarefaction) and extrapolated diversity of vocalising species for each study site based on the number of sound recordings in which each species was present (abundance of vocalisations). After the extrapolated curves for all sites reached a horizontal asymptote, all confidence intervals (95%) overlapped. This indicates no significant difference in vocalising species diversity between sites ($p > 0.05$). Fig. 4 displays similar information as Fig. 3, but exclusively for vocalising bird species. However, after horizontal asymptotes for all sites were reached, all confidence intervals (95%) overlapped again, indicating no significant difference in vocalising bird diversity between sites ($p > 0.05$).

After analysing data obtained during the transect surveys, 9.78% of the surveyed transects turned out to consist of swamp habitat and 74.83% consisted of terra firma forest habitat. In swamps, 0.57 signs of human activity were found per kilometre, whereas 1.56 signs/km were found in terra firma forest habitat. Hunting activity was only observed in terra firma forest (0.74 signs/km). Non-hunting activity, on the other hand, was found in both swamp (0.57 signs/km) and terra firma forest (0.82 signs/km) habitat. During mammal surveys, a total of 27 different mammal species were recorded across all sites. Numbers of mammal species surveyed in La Belgique, La Palestine, and Ngouleminanga were 16, 13, and 25, respectively. Signs were more abundantly observed in swamp habitat (39.25 signs/km) compared to terra firma forest habitat (17.19 signs/km). A Welch ANOVA test indicated overall significant differences between the sites ($F = 4.97$, $p = 0.036$); however, a pairwise Games-Howell post-hoc analysis showed no significant differences in mammal abundance between any of the study sites ($p > 0.05$ for comparisons between all sites). Similarly, there were no significant differences in the abundance of mammals detected in the audio files between any of the study sites (One-way ANOVA test: $F = 2.43$, $p = 0.122$). Furthermore, mammal species diversity among study sites based on the number of signs observed per species indicated a significantly higher mammal species diversity in Ngouleminanga compared to La Palestine ($p < 0.05$). During bird surveys, a total of 42 different bird species were recorded across all sites. Similar levels of bird abundance were noted in different habitats, with 32.43 bird signs/km in swamps and 21.60 bird signs/km in terra firma forests. The numbers of bird species surveyed in La Belgique, La Palestine, and Ngouleminanga were 23, 24, and 30, respectively. However, these differences were statistically non-significant (One-way ANOVA test: $F = 0.94$, $p = 0.414$). In regards to the diversity of the observed species during bird surveys, no significant difference in bird species diversity was found between the study sites ($p > 0.05$). Encounter rates for all identified species are presented in Tables 4 and 5 of the SI.

When evaluating how all measured factors affected biological sounds in terms of vocalisation abundance, GEE revealed that significantly less mammal and bird vocalisations were recorded on days with high amounts of rainfall (Wald $= 16.29$, $p = 5.4e{-}05$ for mammals; Wald $= 15.47$, $p = 8.4e{-}05$ for birds) (Table 6 of the SI for mammals; Table 7 of the SI for birds). Rainfall was the only significant driver of bird vocalisation abundance, whereas the abundance of mammal vocalisation was also negatively affected by the percentage of swamp in the area (Wald $= 9.19$, $p = 0.002$). Furthermore, the amount of human activity proved to negatively affect mammal vocalisation abundance (Wald $= 4.84$, $p = 0.028$).

GEE were also used to uncover the drivers of bioacoustic diversity. Diversity of mammal vocalisations was driven by multiple factors (SI Table 8). First of all, human activity negatively affected the diversity of vocally-active mammals (Wald $= 5.50$, $p = 0.019$). Second, as with abundance, the diversity of vocally-active mammals was negatively affected by the percentage of swamp that covered
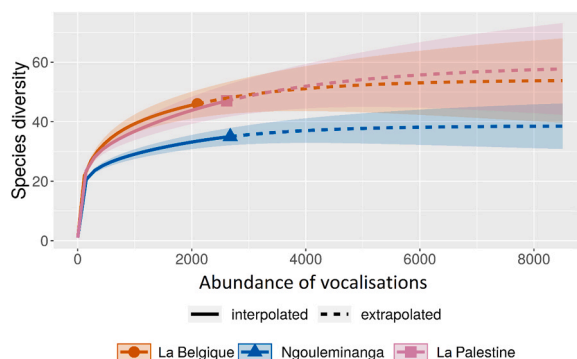
Fig. 3. Rarefaction curves (and 95% confidence intervals) comparing the diversity of vocalising species across study sites, extrapolated until all curves reached a horizontal asymptote. The diversity of vocalising species does not significantly differ between study sites ($p > 0.05$) because confidence intervals overlap.
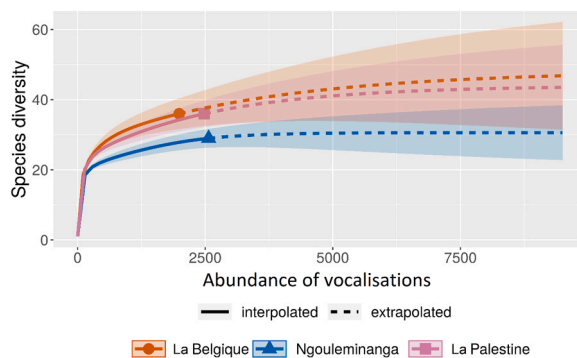
Fig. 4. Rarefaction curves (and 95% confidence intervals) comparing the diversity of vocalising bird species across study sites, extrapolated until all curves reached a horizontal asymptote. The diversity of vocalising bird species does not significantly differ between study sites (p > 0.05) because confidence intervals overlap.

the area (Wald = 8.38, p = 0.004). Lastly, rainfall had a negative effect on the diversity of vocally-active mammals (Wald = 25.40, p = 4.7e-07). The vocalisation diversity of birds was driven by other factors (SI Table 9). First, temperature negatively affected the diversity of vocalising bird species (Wald = 6.02, p = 0.014). In addition, the vocalisation diversity of bird species was positively affected by the abundance of birds measured during field surveys (Wald = 8.52, p = 0.004).

4. Discussion

The listening process helped to identify a total of 52 vocalising bird and mammal species in sound recordings. For birds, this number is similar to the number of species that were observed during our transect surveys. This trend has often been observed when comparing monitoring methods for birds (Sedláček et al., 2015; Wheeldon et al., 2019; Blake, 2021). For mammals, the number of species observed in the transect surveys was higher, because not all mammal species vocalise (Buxton et al., 2018). Some rare species that are known to occur in the area were not detected. Deploying more sensors to cover a larger section of the landscape or recording over a longer period of time will increase the chance of detecting these species. For a detailed overview of species detected with both or either method, see Figs. 5 and 6 of the SI. Passive acoustic monitoring was previously used to study one or multiple vocalising species in Ivory Coast (Heinicke et al., 2015), the Central African Republic (Thompson et al., 2010a), Gabon & Republic of Congo (Wrege et al., 2017), and Ghana (Thompson et al., 2010b). These studies, together with our study, are early investigations documenting vocalising bird communities using both field and acoustic survey methods. However, to our knowledge, this is the first study that provides an inventory of the entire vocalising mammal community in an African tropical rainforest. Therefore, we provide baseline information regarding the community of vocally-active mammals in the area.

After the contribution to the soundscape across animal classes was evaluated, we found that insects were the most vocally-active animal class. Birds also showed higher vocalisation rates than mammals and amphibians, who did not differ from each other. Insects were detected in every sound recording, which suggests that they produce sounds continuously. Amphibians, on the other hand, vocalised predominantly at night. Possible explanations for the difference in vocalisation rates between birds and mammals are that birds communicate more vocally than mammals, or that birds are more conspicuous in their vocalisations. The observed dominance of insects in a tropical soundscape is compliant with other studies (Aide et al., 2017; Ferreira et al., 2018). Overall, the hypothesis that animal classes do not contribute equally to the soundscape is supported. Moreover, these findings suggest that the community of vocally-active animals in tropical forests is dominated by insects and birds, although mammals and amphibians also contribute to the soundscape. As quantitative assessments of the relative contribution of different taxonomic groups to tropical soundscapes are scarce, this knowledge may improve understanding of ecological interactions among animal communities (Ferreira et al., 2018).

In regards to the abundance of vocalisations along a disturbance gradient, vocalisation rates between La Palestine and Ngouleminanga did not differ, whereas vocalisations were significantly less abundant in La Belgique compared to the other sites. This can mainly be attributed to differences in bird vocalisation abundance between sites. This finding was not reflected by the transect surveys, which indicated no difference in bird abundance between study sites. Thus, vocalisation abundance is not necessarily proportional to species abundance. For mammals, most species that showed differences in vocalisation abundance between sites vocalised most abundantly in La Belgique and are known to be prone to hunting pressure (Dadem et al., 2018; Maisels et al., 2019; Vanthomme et al., 2013). Therefore, it is likely that the species were more abundant in La Belgique because hunting pressure is low in that area (Tagg et al., 2011). Another explanation is that these mammals are more vigilant, thus producing less vocalisations, in areas with more hunting activity (Croes et al., 2007). Correspondingly, most bird species that vocalised more in La Belgique are known to avoid habitat under anthropogenic pressure (Chasar et al., 2014; Languy, 2019; Tamungang et al., 2013). In addition, most bird species that showed higher vocalisation abundance in La Palestine and Ngouleminanga are either unaffected by human disturbance or prefer forest edge or other habitat that is present in these sites (Dale et al., 2000; Beier et al., 2002; Péron and Crochet, 2009; Okosodo et al., 2016; Holbech et al., 2018; Languy, 2019). The finding that vocal abundance was higher in more disturbed areas can also be attributed to the fact that birds adjust their vocal behaviour in response to anthropogenic noise (Hu and Cardoso, 2010). Therefore, birds might increase their

vocalisation rates when exposed to high levels of anthropogenic disturbance. Altogether, the results support the hypothesis that the structure of biological sounds varies along a disturbance gradient. Overall, species seem to vocalise most abundantly in sites that accommodate their preferences. Besides the explanation that the level of disturbance does not affect mammal vocal abundance, it is also possible that disturbance in the study area is not strong enough to affect mammal vocalisations. Naturally, intraspecific variation, which causes individuals of the same species to react differently to environmental stressors, could also drive differences in vocalisation abundance (Harding et al., 2019). Studying this variation requires recognition of individuals within a species, which is beyond the scope of this research, but might provide deeper insights into the vocal behaviour of species along a disturbance gradient.

With regard to the diversity of vocalisations, no differences were found between the study sites. The same is true for vocalisation diversity of birds only. This suggests that the disturbance gradient did not affect vocalisation diversity in the study area. For birds, the similarity in vocalisation diversity between disturbance levels is reflected by the transect survey results. In contrast, the transect survey did show differences between the sites in mammal diversity. This contrast can be explained by the fact that visual and acoustic measurements detect different mammal species (Buxton et al., 2018). However, studies mainly showed a negative impact of anthropogenic noise on vocalisation diversity (Francis et al., 2011; Perillo et al., 2017). Thus, the results contradict the expectation that the structure of biological sounds varies along a gradient of disturbance and indicate that the level of disturbance does not impact the diversity of vocalising species. However, disturbance factors in the area, like anthropogenic noise, may not have reached the threshold beyond which vocalisation diversity is negatively affected. Another possible explanation is that the lack of difference along the disturbance gradient is caused by homogenisation of the biodiversity (Burivalova et al., 2019). In this case, the loss of specialised species due to disturbance is compensated by an increase in the number of generalist species in the area (Burivalova et al., 2014). Future research towards the level of disturbance needed to alter vocalisation diversity and the possible influx of habitat generalists in the area is needed to point out the exact reasons behind the unaffected vocalisation diversity along the disturbance gradient.

After assessing possible drivers of biological sounds, GEE showed that vocalisation abundance throughout the area was negatively impacted by rainfall. Mammal vocalisation abundance was also negatively affected by hunting pressure and the amount of swamp habitat in the area. The negative impact of rainfall indicates that, even though recordings where rain was heard were removed from the dataset, both mammals and birds still vocalised less on days with more rainfall compared to days with less rainfall. The reduction in vocal activity due to rain is in line with previous studies showing that both vocalising mammals and birds call less frequently in periods after rainfall (Clink et al., 2020; Ducrettet et al., 2020). Thus, rainfall drives biological sounds by lowering the vocalisation abundance of mammal and bird species. The negative impact of human activity on vocalisation abundance was only found in mammals but not in birds. Therefore, it is possible that anthropogenic pressure has a heavier impact on mammals than on birds. Hunting is known to impact the density and vocal behaviour of both mammal and bird populations in tropical forests (Redford, 1992; Brumm, 2004; Croes et al., 2007). However, hunting pressure negatively affects mammal abundance to a higher degree than bird abundance (Benítez-López et al., 2017). Therefore, human activities prove to drive biological sounds; however, their magnitude in the area may only be strong enough to influence mammal vocalisation abundance. The finding that swamp habitat only affected vocalisation abundance of mammals is supported by the result that over twice as many mammal signs were found per kilometre of swamp compared to the number of signs found in terra firma forests. Birds, on the other hand, were observed in equal numbers throughout different habitat types. This suggests that mammals prefer swamp habitat or use it as a refuge. This pattern can be explained by the finding that human activities were more abundant in terra firma forests than in swamps. Moreover, hunting signs were completely absent in swamp habitat. Higher mammal abundance in swamp habitat, in turn, can provide an explanation for the negative impact of swamp habitat on mammal vocalisation abundance. Indeed, the increase in mammal abundance, caused by low anthropogenic pressure in this habitat, may affect species interaction dynamics within the swamp community, resulting in increased predation risk. These altered interaction dynamics can heighten the vigilance of vocalising mammals, which explains the lower vocalisation rates observed in areas with more swamp habitat. This proposition is in line with the current knowledge that increased animal density strengthens interactions, such as predation, between species (Kordas and Dudgeon, 2011; Jhala and Isvaran, 2016). Predation, in turn, is known to induce vigilance, which leads to a decrease in vocalisations (Croes et al., 2007). Hence, swamp habitat affects vocalisation patterns seemingly because limited anthropogenic influence in this habitat induces high mammal abundance.

The amount of human activity, swamp habitat, and rainfall all negatively impacted the diversity of mammal vocalisations. Bird vocalisation diversity, on the other hand, was negatively affected by temperature and positively affected by the abundance of birds in the area. For mammals, the same factors that impacted the abundance of mammal vocalisations also affected the diversity of their vocalisations. Therefore, it is likely that human activity and swamp percentage reduce both vocalisation abundance and diversity in mammals in similar ways (Croes et al., 2007; Laurance et al., 2008; Jhala and Isvaran, 2016; Benítez-López et al., 2017). As for rainfall, if species vocalise less in periods of heavy rain, then fewer species will be detected at specific recording times. This results in a lower diversity of mammal vocalisations due to rain. Why rainfall did not drive the diversity of bird vocalisations is unknown. It is plausible that, because bird vocal diversity was generally higher than mammal diversity, reduced vocal behaviour after periods of rain was relatively more apparent in mammals than in birds. The fact that temperature turned out to be a driver of vocalisation diversity in birds means that fewer bird species were detected on days with higher average temperatures. This effect of temperature on vocalisation diversity was also mentioned by McGrann and Furnas (2016), who suggested that many bird species reduce their vocal activity on hot days to save energy. Thus, temperature incurs a limited number of bird species detections and, therefore, a lower vocalisation diversity. Another driver of diversity in bird vocalisation is bird abundance. Hence, in places where more birds were encountered, more bird species vocalised. A logical explanation for this would be that when the total number of birds in an area increases, the chance of different species being present and displaying vocal behaviour also increases. This reasoning is in line with the deduction of Depraetere et al. (2012), who concluded that local animal diversity is reflected in the soundscape. In contrast, mammals showed less vocal behaviour in areas where they were more abundant. This suggests that high bird density does not result in interactions which impede

the vocal activity of bird species, but this scenario is plausible for the mammal community.

Not all the measured predictor variables that were expected to drive biological sounds turned out to do so. Mammal abundance, accessibility, remoteness, and percentage of terra firma forest all had no impact on biological sounds. As for mammal abundance, species that were identified during mammal abundance surveys were mostly different (non-vocalising) from the mammal species that were recorded by the sensors. This could explain why, overall, mammal abundance did not drive abundance or diversity of mammal vocalisations. Another explanation is that species interactions that were shaped by the overall level of wildlife abundance did not have any impact on mammal vocalisation patterns. The distance between a sensor and the nearest trail and between a sensor and a village, which represent the accessibility and remoteness of an area, respectively, did not alter biological sounds. Due to different types of land-use throughout the study area, proximity to a trail or village might not always imply the same type of impact. For instance, the trails in Ngouleminanga may be more frequently used by hunters compared to the trails in La Belgique, a site dedicated to research activities. Hence, accessibility and remoteness result in very different types and levels of anthropogenic impacts throughout the study area, with no clear overall pattern. In addition, low numbers of sites and sensors do not allow for the use of contextual variables and multilevel models (Maas and Hox, 2005); this limits the ability to detect patterns regarding these factors. Therefore, a similar study with a higher sample size (number of study sites and sensors) is needed to uncover the exact impact of factors with contextual effects. Lastly, the amount of terra firma forest in the area near a sensor did not alter biological sounds. Compared to swamp habitat, which affected biological sounds, terra firma forests had a lower mammal abundance and more human activities. The reason why the amount of terra firma habitat did not affect vocalisation patterns despite high levels of human activities in these habitats remains unclear. More studies are needed to further assess the impact of this variable. Despite the fact that not all predicted drivers proved to affect biological sounds, the results confirm the hypothesis that anthropogenic and environmental factors drive vocalisation patterns. Moreover, it can be inferred that anthropogenic disturbance both directly and indirectly drives vocalisation patterns; directly, by altering animal behaviour in reaction to human activity and indirectly, through its effect on the animal community structure. Results also suggest that animal community structure (and therefore biological sounds) is driven by the available habitat. Additionally, vocalisation patterns are impacted by weather conditions.

Despite the fact that some predictor variables were found to be drivers of biological sounds, one should keep in mind that these drivers might affect biological sounds through processes that were not covered by this study. For instance, anthropogenic disturbance is also known to impact the climate and habitat structure (Ellis, 2011). If this is the case in the study area, it may indirectly affect biological sounds. Additionally, other drivers that were not included in this study might have an effect on the structure of biological sounds as well. If a vocalising species occurs at similar densities in all sites while its vocalisation rate varies among sites, this is likely due to intraspecific variation in behaviour in response to site-specific factors (Harding et al., 2019). The lack of data on intraspecific variation is a limitation of this research. Intraspecific variation can cause individuals to behave, and thus vocalise, differently under different kinds of disturbances (Harding et al., 2019). This phenotypic plasticity can result in adjusted vigilance, as mentioned before, but also in other behavioural survival and mating tactics (Wong and Candolin, 2015). Research that accounts for intraspecific behaviour variation will shine more light upon the drivers of biological sounds.

5. Conclusion

Overall, insects and to a lesser extent birds were the most dominant animal classes in the soundscape. In addition, the structure of biological sounds proved to vary along a gradient of disturbance. Mammal acoustic activity did not vary among sites with differing levels of disturbance, whereas acoustic activity of birds did. The vocalisation abundance of birds was lowest in the site where anthropogenic disturbance was least present. Thus, we suggest that birds vocalise more abundantly in sites with more anthropogenic disturbance. Furthermore, as expected, anthropogenic disturbance affected biological sounds indirectly through its impact on the animal community structure. In turn, animal community structure and weather conditions directly affected biological sounds. Anthropogenic disturbance may also affect biological sounds by altering vocal behaviour of specific individuals and by modifying habitat structure and climate, but further investigations into these impacts are required. These results indicate that the number of acoustically active species and the amount of sound produced vary among animal classes. This highlights that sound sources do not make equal contributions to the soundscape and furthers knowledge of soundscape structure. The results further show that the impacts of anthropogenic and ecological factors on biological sounds vary depending on the sound source, thus suggesting that soundscape components are not affected by soundscape drivers in the same way. Additionally, the sound data we obtained provide baseline acoustic information on the vocalising species which may be used for automated detections of these vocalisations in the future. Our study may contribute to the development of applications that monitor soundscapes and detect important changes in landscapes by adding to the understanding of soundscape drivers and vocalising species. These applications, in turn, can help guide future decision making and landscape conservation planning.

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CRediT authorship contribution statement

Johan Diepstraten: Data collection (lead), Data curation (lead), Formal analysis (lead), Visualization (lead), Writing – original draft (lead), Writing – review & editing (lead), Methodology (equal), Conceptualization (supporting). **Jacob Willie**: Conceptualization (lead), Supervision (lead), Methodology (equal), Data collection (supporting), Data curation (supporting), Formal analysis (supporting), Visualization (supporting), Writing – original draft (supporting), Writing – review & editing (supporting).

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.

Code availability

For custom code, contact the corresponding author.

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Consent to participate

No human participants were involved in the study.

Consent for publication

The authors give consent for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01819.

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