Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea

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Abstract: There is global concern about tropical forest degradation, in part, because of the associated loss of biodiversity. Communities and indigenous people play a fundamental role in tropical forest management and are often efficient at preventing forest degradation. However, monitoring changes in biodiversity due to degradation, especially at a scale appropriate to local tropical forest management, is plagued by difficulties, including the need for expert training, inconsistencies across observers, and lack of baseline or reference data. We used a new biodiversity remote-sensing technology, the recording of soundscapes, to test whether the acoustic saturation of a tropical forest in Papua New Guinea decreases as land-use intensity by the communities that manage the forest increases. We sampled soundscapes continuously for 24 hours at 34 sites in different land-use zones of 3 communities. Land-use zones where forest cover was fully retained had significantly higher soundscapes saturation during peak acoustic activity times (i.e., dawn and dusk chorus) compared with land-use types with fragmented forest cover. We conclude that, in Papua New Guinea, the relatively simple measure of soundscapes saturation may provide a cheap, objective, reproducible, and effective tool for monitoring tropical forest deviation from an intact state, particularly if it is used to detect the presence of intact dawn and dusk choruses.

Keywords: avifauna, bioacoustics, community forest management, forest degradation, hunting, land use planning, subsistence agriculture, vocalizing biodiversity

El Uso del Paisaje Sonoro para Detectar Grados Variables de Influencia Humana sobre los Bosques Tropicales en Papúa Nueva Guinea

Resumen: Existe una preocupación global por la degradación del bosque tropical, en parte, por la pérdida asociada de la biodiversidad. Las comunidades y personas indígenas juegan un papel fundamental en el manejo del bosque tropical y son continuamente eficientes en la prevención de la degradación del bosque. Sin embargo, el monitoreo de cambios en la biodiversidad por causa de la degradación, especialmente a una escala apropiada para el manejo del bosque tropical local, está plagado de dificultades, incluyendo...
Introduction

Worldwide, the majority of tropical forests are used, exploited, or managed in a way that is often crucial for the livelihoods of communities using the forest: about 350 million people globally depend directly on forests for subsistence (FAO 2012). At the same time, any form of forest use changes forest biodiversity, even if complete deforestation is avoided (Chaudhary et al. 2016). Communities and indigenous people play a fundamental role in tropical forest management in terms of area used overall and in type of management (Charnley & Poe 2007; Burivalova et al. 2016). Papua New Guinea is unusual in that 95% of the country’s land is owned by resident communities under a customary land-tenure system recognized in the constitution (Brown & Mayer 2009; Shearman et al. 2009). How each community manages its forest is therefore, collectively, of fundamental importance to the biodiversity and forest conservation nationally, as well as globally, because the island of New Guinea contains the third largest area of tropical forest worldwide (Bryan et al. 2010).

Monitoring biodiversity thoroughly and objectively across sufficient spatial and temporal scales in tropical forests requires a too-often prohibitive amount of time, resources, and expertise, especially for small communities (Magurran et al. 2010). Acoustic surveys and the new discipline of ecoacoustics (Sueur & Farina 2015) represent emerging opportunities to monitor sound-producing species in their habitat without interference by a human observer (e.g., Blumstein et al. 2011; Pijanowski et al. 2011a; Krause & Farina 2016). The resulting recordings represent a lasting, unbiased record of the ecosystem’s soundscapes that can be kept as a reference (Wimmer et al. 2010; Sueur et al. 2014; Truskinger et al. 2014). Obtaining such baselines is especially valuable for ecosystems that are still relatively little modified by humans but are under immediate threats, such as the forests of Papua New Guinea.

Recording entire soundscapes, defined as the collection of all sounds in a certain space over time, could be used to monitor ecosystems (e.g., Dumyahn & Pijanowski 2011; Tucker et al. 2014; Fuller et al. 2015). This would be particularly useful in the forests of Papua New Guinea, where traditional monitoring, for example through point counts, is difficult due to the thick canopy and rugged terrain. Acoustic surveys of avifauna can be more effective than visual surveys in dense vegetation habitats (Celis-Murillo et al. 2012). Many vocalizing species in Papua New Guinea, particularly amphibians and invertebrates, are not yet well known to science; therefore, a monitoring tool that does not rely on species recognition would be particularly valuable.

Specifically, one might assume that natural selection causes species sharing the same acoustic space to partition that space (acoustic niche hypothesis). This partitioning enables efficient communication and is demonstrated by overdispersion of acoustic features in terms of time and frequency (Krause 1987; Pijanowski et al. 2011b). As a result, the more species there are in an area, for example a rainforest, the more saturated one would expect the soundscape to be. Evidence from forest landscapes suggests that various properties of the soundscape, expressed through acoustic indices, can be used as proxies for biodiversity (e.g., Sueur et al. 2008; Gasc et al. 2013; Fuller et al. 2015). This can be particularly useful in cases where expert or automated species recognition is not currently feasible.

Disturbance or degradation of a forest causes changes in the community composition, species richness, or abundance of vocalizing animals, and results in changes in the forest’s soundscape (Sueur et al. 2008; Tucker et al. 2014; Fuller et al. 2015). Although soundscape monitoring is a promising avenue for monitoring of biodiversity and conservation effectiveness, the soundscapes of forests used or degraded by people have been examined in only a handful of studies, mostly in temperate regions (Tucker et al. 2014; Fuller et al. 2015). We investigated the
hypothesis that soundscapes saturation decreases along a gradient of increasing human influence, from pristine to managed tropical forests in the Adelbert Mountains, Papua New Guinea. This research is a step toward developing a low-cost, objective, high-coverage, ecosystem-monitoring tool.

Methods

Study Area and Study Site

We recorded tropical forest soundscapes in the Adelbert Mountains of Papua New Guinea in July 2015. We chose this study site because there are large areas of intact tropical forests that can serve as soundscapes baselines (Rodriguez et al. 2014) for our study and for future reference (Fig. 1). Some communities in this area have managed segments of their land according to a land-use plan for over a decade (Brown & Mayer 2009), which allowed us to investigate soundscapes along a land-use intensity gradient. The Adelbert Mountains span elevations from 150 to 1672 m asl (Webb et al. 2003), and our sampling sites were distributed from 182 to 899 m asl. The ecosystem is a seasonally wet tropical-hill forest that has a wide variety of soil types and 3200–3600 mm of precipitation per year (Shearman & Bryan 2011). The region is representative of the broader Northern New Guinea montane rainforests (Olson et al. 2001).

Our study area included the land of 3 communities: Musiamunat, Yavera, and Iwarame in the Bogia district in the northwestern part of Madang Province (Fig. 1). Each community divided its land into conservation, hunting, forest-use, gardening, agriculture, and village-development zones in 2004 (Musiamunat) and 2007 (Yavera and Iwarame) (Brown & Mayer 2009) with the help of the Nature Conservancy. Since then, the communities have reportedly used the zones for their respective purposes, a claim that matches with our observations and

Figure 1. Study site in the Adelbert Mountain Range of Papua New Guinea showing the border of the 3 focal communities, Musiamunat, Yavera, and Iwarame, from south to north (black lines) that allocated their land to different land uses. Areas with no forest, based on a supervised classification of SPOT satellite image, are due to anthropogenic deforestation and natural landslides. The red square in the insert map shows the extent and location of the study site.
personal communications while working in the area (see Supporting Information for details on land-use zones).

Data Acquisition

We selected 34 sampling sites to represent all main land-use zones within each of the three communities (Fig. 1). Our sampling sites were at least 300 m from zone edge and at least 30 m from any path. At each site, we installed an acoustic recorder (Frontier Labs, Bioacoustics Recorder, specifications in Supporting Information). Each mono recorder was scheduled for autonomous recording and had an integrated GPS for location and time synchronization. The soundscapes at each site were recorded for at least 24 hours. Inputs were saved on secure digital (SD) cards in the Waveform audio file format. The recorders were set to record continuously in 30-min segments at 40 dB gain and with a 44 kHz sample rate. Due to limited amount of time, the number of recorders available (10), and arrangements with the communities, we adopted a staggered sampling design: each day we deployed 5 recorders. All recordings were obtained from 2 to 11 July 2015 (Supporting Information). To account for the potential influence of the day of recording, on each day of deployment, we covered different land-use zones and elevations. The weather conditions were similar during the data acquisition (little rain, low winds). Statistically, we took the day of the recording into account by including it as a random factor in all models. We carried out our study during the 2014–2015 El Niño event, which caused unusual precipitation patterns; Papua New Guinea had a severe drought (https://www.climate.gov/news-features/blogs/enso/march-2016-el-nino-1-2/35%2Blocal-update-spring-forward [accessed May 2017]).

There was little anthropogenic sound in our study region because there are no roads and little airplane traffic, which made the study of biophony (animal sounds) easier (Farina 2014; Sueur et al. 2014). At each sampling site, we recorded the following information: elevation, canopy-cover estimate, slope, details of reported land use, and temperature (Table 1).

Signal Processing

We used the methods of Truskinger et al (2014) to analyze the audio recordings and summarize them here. We divided the source-audio files into 1-min segments, each resampled to 22050 Hz, and converted to a spectrogram with a short-time Fourier transform with a nonoverlapping window of 512 samples. We converted spectral amplitude values (A) to decibels with dB = 20 × log(A). The resulting spectograms had 256 frequency bins spanning 11,025 Hz (≈43 Hz per bin). All programs were written in C#, and computations were performed with dual Intel Xeon E5-2665 CPUs (32 virtual cores running at 2.4 GHz, 256 GB DDR3 RAM, 3 TB Small Computer System Interface Raid, and dual 1 GB Ethernet Network Interface Controllers).

Calculation of Soundscape Saturation

We defined soundscape saturation, $S_m$, as the proportion of frequency bins that are acoustically active in a given minute, $m$. We used a combination of two acoustic indices to determine whether a particular frequency bin was acoustically active or not. An acoustic index is a function describing the distribution of acoustic energy and its complexity in terms of time, frequency, signal-to-noise ratio, etc. For each frequency bin $f$ in each 1-min $m$ spectrogram, we calculated acoustic indices $BGN_{mf}$ (background noise) and $POW_{mf}$ (power). Given a window of 512 samples and a sampling rate of 22,050 Hz, each frequency bin therefore contained 2,584 spectrogram cells. Noise removal from raw spectograms is typically achieved by subtracting the mean, median, or mode of the decibel values in the relevant frequency bin or neighborhood. We used the mode of the distribution of decibel values in any frequency bin as the value for its $BGN$ index,

$$BGN_f = \text{Mo}(dB_{f}),$$

where $c$ and $f$ index the decibel values in all the spectrogram cells, $c$, of frequency bin $f$; Mo is mode (Towsey et al. 2014); and dB is decibel. The term noise does not refer to anthropogenic noise but rather to the most common continuous baseline of acoustic energy in any frequency bin over 1 min. Very often, the BGN component of acoustic energy comes from insect choruses that are typically continuous, narrow-band events.

Once $BGN_f$ is calculated, the value of $POW_f$ is given by

$$POW_f = \text{max}(dB_{f} - BGN_f),$$

where $c$ is an index over all the 2584 cells in frequency bin $f$. The $POW_f$ is similar to the signal-to-noise ratio (SNR) of the acoustic signal in bin $f$. In environmental recordings, contributions to $BGN_f$ and $POW_f$ can come from the same source. For example, where crickets are evenly distributed through the landscape around a sensor, there will be a background murmur of crickets that contributes to BGN as well as the discrete chirps of crickets close to the microphone that may contribute to $POW_f$ in the absence of louder sources.

Because all recordings were longer than 24 hours (mean length = 38 hours; Supporting Information), we took an average of the $POW_f$ and $BGN_f$ values for the minutes of the day that were duplicated. This resulted in 1440 $POW_f$ and $BGN_f$ values for each of the 34 sites.
Having calculated values of $BGN_{mf}$ and $POW_{mf}$ for each recording, we then calculated a binary variable $a_{mf}$:

$$a_{mf} = 1 \text{ if } (BGN_{mf} > \theta_1) \text{ or } (POW_{mf} > \theta_2); \quad \text{otherwise}, \quad a_{mf} = 0.$$  

(3)

Here $\theta_1$ and $\theta_2$ are thresholds, the values of which are set so that frequency bin $f$ of minute $m$ is acoustically active when $a_{mf} = 1$ and inactive when $a_{mf} = 0$. We tested values for $\theta_2$ from 4 to $8 \text{ dB}$ in steps of $1.0 \text{ dB}$ and $\theta_1$ from $80\%$ to $99\%$ in steps of $2\%$ that yielded a near-normal distribution of $S_m$ (soundscape saturation) values over all the recording minutes from all sites. This was achieved with a value of $\theta_2 = 6.5 \text{ dB}$ and $\theta_1 = 90\%$ percentile dB value derived from the distribution of all $BGN_{mf}$ values.

Finally, $S$ for minute $m$ ($S_m$) is given by the fraction of frequency bins with value $a_{mf} = 1$:

$$S_m = \sum_f a_{mf} / N,$$  

(4)

where the sum is over all $N$ frequency bins ($N = 256$). To achieve a reasonable degree of smoothness of $S_m$ values across time and decrease the importance of outliers, we used a 5-min sliding window: $S_m = (S_{m-2} + S_{m-1} + S_m + S_{m+1} + S_{m+2}) / 5$.

Table 1. Overview of explanatory variables used in model selection to explain difference among sites in soundscape saturation.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>environmental; continuous, square root transformed</td>
<td>elevation above sea level, range 182–899 m, mean 381.7 m</td>
</tr>
<tr>
<td>Slope ($^\circ$)</td>
<td>environmental; continuous, square root transformed</td>
<td>slope as estimated in the field, range $0^\circ$ to $-45^\circ$, mean $13.14^\circ$</td>
</tr>
<tr>
<td>Community</td>
<td>human impact; categorical</td>
<td>3 categories: Iwaram, Yavera, Musiamunat; could differ in the degree to which they enforced land use in each zone and in population density</td>
</tr>
<tr>
<td>Land-use zone</td>
<td>human impact; categorical</td>
<td>5 categories: cacao plantation, gardening, forest use, hunting, conservation</td>
</tr>
<tr>
<td>Size (ha)</td>
<td>human impact; continuous, log$_{10}$ transformed</td>
<td>size of a designated land-use zone, measured from a map, range 1.2–1630 ha, mean 281 ha; gardening and cacao zones not fully converted</td>
</tr>
<tr>
<td>Continuous forest cover</td>
<td>human impact; categorical</td>
<td>binary, forest cover in the immediate vicinity of sampling site (within 10-m radius) determined in the field; simplification of the variable land-use zone whereby conservation, hunting, and forest use have continuous forest cover; gardening and cacao plantation have fragmented forest cover</td>
</tr>
<tr>
<td>Deforestation within 500 m</td>
<td>human impact; continuous, square-root transformed</td>
<td>percent deforested land within a 500-m radius of the sampling site, determined from a satellite-image classification</td>
</tr>
<tr>
<td>Distance to village (m)</td>
<td>human impact; continuous, square-root transformed</td>
<td>distance on the satellite image to the nearest village, does not reflect actual walking distance, range 507–5689 m, mean 2137 m</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>human impact, square-root transformed</td>
<td>quantified from canopy cover photographs; used only in separate analyses for continuous and fragmented forest sites</td>
</tr>
<tr>
<td>Deforested area (ha)</td>
<td>human impact, square-root transformed</td>
<td>size of the garden or cacao plantation patch, calculated from the satellite image; used only for analysis of sites with fragmented forest cover</td>
</tr>
<tr>
<td>Distance to continuous forest (m)</td>
<td>human impact, square-root transformed</td>
<td>distance on the satellite image to the nearest continuous forest area; used only for the analysis of sites with fragmented forest cover</td>
</tr>
<tr>
<td>Closest zone</td>
<td>human impact, categorical</td>
<td>closest neighboring land-use zone (5 categories, see above); used only for analysis of sites with fragmented forest cover</td>
</tr>
</tbody>
</table>

Statistical Analyses

To account for the fact that acoustic activity, and therefore soundscape saturation, changes with time of day, we fitted all candidate models to each minute of the day separately. To determine if the variables describing human impact shape soundscape saturation at our sampling sites, and if so which ones, we used the information-theoretic approach to model selection (Burnham & Anderson 1998). As opposed to traditional hypothesis testing, this approach let us compare the likelihood of different candidate models, given our data set, and the relative importance of every variable. Apart from anthropogenic variables, we also included environmental variables, such as elevation, that we expected might influence the soundscapes (Table 1). We quantified the amount of forest fragmentation (not necessarily due to anthropogenic activities but also to landslides) in the vicinity of our sampling sites by carrying out a supervised classification of a high resolution SPOT7 satellite image (from 3 June 2015, details in Supporting Information).

First, we defined a set of candidate linear mixed models, which were all possible simplifications of the full model with day of recording as a random effect: $S_m = \text{elevation + slope + community + land-use zone + size of land-use zone + continuous forest cover + deforestation within 500 m + distance to village}$. 
There are $2^n$ possible candidate models, where $n$ is the number of noninteracting variables. We had 256 candidate models and a null model, which had no variables. Due to a small sample size (34 sites), we did not fit interactions. Every time we fitted the candidate models to a response variable data set (separately for each minute), we selected the most parsimonious model, based on the Akaike information criterion adjusted for small sample size (AICc) (Akaike 1973; Burnham & Anderson 1998). We evaluated the relative variable importance for all variables based on the Akaike weights of the models in which each variable occurred. This meant that, for example, if the variable elevation occurred in the majority of the top-10 models, it would have a high relative variable importance (max. 1), and we would conclude that it played an important role in shaping the soundscape saturation. Conversely, if a variable occurred predominantly in models with low Akaike weights, it would have a relative variable importance tending toward zero.

We also performed a separate set of analyses for sites with continuous forest cover and those without for the following reasons. There were four variables that were relevant only to sites with fragmented forest cover (Table 1, last four rows): estimate of the remaining canopy cover (all sites with continuous forest cover had a high canopy cover, 80–95%, whereas canopy cover in fragmented sites was 0–50%); area of the cleared patch; distance to the nearest continuous forest; and type of the closest neighboring land-use zone. The values of these variables deviated substantially from a Gaussian distribution in a way that could not be addressed by a transformation; hence, we used them only in the separate analysis of the sites without continuous forest cover (the low level of variation did not justify including these variables in the analysis of sites with continuous forest cover). We followed the same model-selection procedure as for the main analysis to establish whether any of these variables play an important role in predicting soundscape saturation at sites with and without fragmented forest cover. Due to the low sample size, we considered only models with up to 3 variables and no interactions. We carried out all statistical analyses in R (R Development Core Team 2011).

Results

Soundscape Saturation

We recorded and processed 1299 hours of soundscapes. All data are publically accessible, as well as photographs of each site, at a repository of bioacoustic recordings (https://www.ecosounds.org/). Soundscape saturation was nonrandomly distributed during the day at each site (Supporting Information). The mean soundscape saturation per site per day ranged from 34 to 74%. Although all sites had at least some minutes during which the soundscape was fully saturated (100%), especially during the times of the highest acoustic activity (dawn and dusk choruses), the number of minutes at each site where saturation was >90% ranged from 7 to 316 min/day.

Soundscape Saturation and Landscape Variables

The null model was most frequently the best (13.8% of the 24-hour period), particularly from about 0530 to 0800 and from 0800 to 1630. The next most frequently (12.6%) superior model was one that included the single binary variable, continuous forest cover, specifying whether forest cover at a site was continuous or fragmented (Fig. 2, Table 1, & Supporting Information). This model was the most parsimonious especially from 0600 to 0800 (dawn chorus) and from 1730 to 2000 (dusk chorus). The remaining models were ranked as most parsimonious fewer than 10% of the time and inconsistently across the 24-hour period. The model saturation equals continuous forest cover had a relatively high explanatory power (adjusted $R^2$ up to 0.55). Throughout the day, sites with continuous forest cover (conservation, hunting, and forest-use zones) had a higher soundscape saturation than sites with fragmented forest cover (gardening and cacao zones), with a brief exception around 0200 and 1930 (Fig. 2).

From about 1830 to 0530, elevation, community, and distance to village played the most important role, and slope and size of the land-use zone had some role (Supporting Information). From 0530 to 0800 (broadest peak in soundscape saturation at forested sites), the land-use zone and how far from the village the site was were the most important variables, in addition to whether the site had continuous forest cover. From about 0800 to 1830, the variable importance seemed to be low or inconsistent, with the exception of whether the site had continuous forest cover. Slope and the amount of deforestation in a 500-m radius of the recording site did not seem to have much importance at any period during the day.

Fragmented Forest Cover

For sites with fragmented forest cover, the null model was also most frequently the best. The area of the cleared patch was the only variable in the second most frequently selected model in sites with fragmented forest cover (gardens and cacao plantations) but had an intermittent predictive ability throughout the day. In contrast, the distance to continuous forest had a consistently high relative importance during a short period, the dawn chorus (Fig. 3). During the dusk chorus and until about midnight, estimated canopy cover had a very high relative variable importance (Fig. 3). For the vast majority of the day, shorter distance to continuous forest and higher canopy cover were both correlated with higher soundscape saturation.
Figure 2. Parameter estimates for the most parsimonious model (soundscape saturation equals continuous forest cover) during peak acoustic activity (points, parameter estimates for sites with continuous and fragmented forest cover; gray, 95% confidence intervals [continuous forest sites]; pink, fragmented sites). The model was fitted separately to each of 1440 min of the day with a 5-min smoothing window.

Continuous Forest Cover

The model saturation ~ elevation was almost as frequently the best model as the null model (11.8% and 12.3%, respectively). During most of the day, forested soundscapes were more saturated at higher elevations (Fig. 4). The model saturation ~ size of the land-use zone was also very frequently the best model (10%). Both elevation and the size of the land-use zone seemed to be particularly important for soundscape saturation from about 1800 to about 0700 (Supporting Information). Larger land-use zones were correlated with higher saturation; however, elevation and land-use zone size were loosely correlated with each other (adjusted $R^2 = 0.30$), resulting into some degree of colinearity in our analysis. Whether a forested site was hunted or used in other ways did not play an important role in terms of soundscape saturation.

Discussion

We recorded and quantified the saturation of 34 different soundscapes in the Adelbert Mountain Range of Papua New Guinea (Fig. 1), including sites in a pristine forest, which can be considered as baseline recordings for future studies of human impact on biodiversity. The habitats ranged from pristine forest set asides for conservation, to hunting zones, and to gardens and small cacao plantations, which represented a gradient of intensity of forest use typical for the Adelbert Mountains. Soundscape saturation showed two distinct peaks during the day, corresponding to the dawn and dusk chorus from about 0400 to 0700 and then from about 1830 to 1930 respectively (Fig. 2 and Supporting Information). It is also during these times that the sites varied the most among each other and when variables linked to human impact had the greatest influence on soundscape saturation. This may help future researchers prioritize recording times in long-term studies when battery life or data storage may be a limitation.

Having considered a range of candidate models, we found that whether a forest is continuous or fragmented explains best the variation in soundscape saturation during the dawn and dusk choruses (Fig. 2). Higher soundscape saturation at sites where forest cover is continuous (conservation, hunting, and forest-use zones) could be both due to a high number of vocalizing species and individuals present (Pijanowski et al. 2011b) and to a more efficient partitioning of the acoustic space by undisturbed communities (i.e., the acoustic niche hypothesis [Krause 1987]). Reduced soundscape saturation suggests
that even mild human activity that involves fragmenting the forest cover (gardening and cacao plantations) substantively diminishes vocalizing biodiversity and effectively eliminates the dawn and dusk chorus. This finding agrees with traditional surveys of avifauna in Papua New Guinea (Marsden & Pilgrim 2003; Marsden et al. 2006) but not necessarily with findings from other tropical regions, such as Costa Rica, where local species richness in forests modified by low-intensity agriculture does not differ significantly from pristine forest (Frischkoff et al. 2014). This has important implications. With respect to biodiversity conservation, it appears beneficial that the communities actively plan and clearly separate land used for subsistence or commercial production from land used for conservation and land uses compatible with complete forest cover, such as hunting.

Soundscape saturation at sites with fragmented forest cover was correlated with different variables in the morning and in the evening (Fig. 3). During the dawn chorus, shorter distances to continuous forests were associated with higher soundscape saturation. This may be due to a great abundance of forest birds that may nest in the forest and venture into the nearby gardens to forage but not into gardens that required crossing relatively large cleared areas. During the dusk chorus, a high number of trees left standing correlated to a high level of soundscape saturation. These trees are often old and large and serve as perching sites for many birds, which likely contributes to higher soundscape saturation. A study of the avifauna on the island of New Britain showed that gardens that had trees attracted large numbers of the parrot *Eclectus roratus* (Marsden & Pilgrim 2003). Others have found that sound diversity is well explained by the vertical vegetation structure (Boelman et al. 2007; Pekin et al. 2012; Rodriguez et al. 2014).

For most of the day, soundscapes of sites with continuous forest cover were more saturated at higher elevations (Fig. 4). Traditional avifaunal surveys in the Adelbert
Mountain Range show that elevation is the most important factor in explaining differences in bird communities. Additionally, a major change in bird communities occurs around 1200 m asl, but this elevation was beyond our sampling scope (Diamond 1972, 1973). Apart from elevation, the size of the land-use zone also appeared to be important. The largest forested land-use zones were at the highest elevation, which resulted in colinearity (adj. $R^2$ of the model elevation equals size of land-use zone was 0.30). Although it is biologically plausible that both elevation and the size of a zone play an important role in the soundscape saturation, we argue that size may currently be less important in the context of our study site. Most forested land-use zones, especially in Yavera and Musiamunat, are connected to other forested zones and a large piece of continuous forest beyond the communities’ land, including even the smallest conservation zones (about 150 ha). Size may become more important in the future if entire land-use zones dedicated to agriculture are converted to gardens or plantations. Complete isolation of forest fragments, which would presumably make size very important, may happen sooner in the case of the smaller zones in the Iwarame community, which has a higher population density than the other communities, likely resulting in stronger pressure on natural resources. A study in the nearby coastal area close to Madang showed that avian diversity increased as the size of forest fragments increased; however, even at 1200 ha fragments did not reach the avian biodiversity levels of a continuous forest (Sam et al. 2014).

An obvious limitation of using soundscapes is that not all species vocalize. Whereas all biodiversity monitoring methods are taxonomically limited, there may be a particular bias in using soundscapes, whereby more secretive, quiet species, difficult to capture on recordings, might be disproportionately endangered by human activities. The detection probability of vocalizing biodiversity likely differs across habitats: sound travels farther and is less distorted in open habitats, such as gardening zones, than in mature rainforest. Future research will provide ways to account for such bias (Darras et al. 2016).

We recorded the soundscapes during an unusual time. The 2014–2016 El Niño event caused the rate of precipitation to be below average during the time of our study. The resulting drought likely affected the behavior and survival of many species. To be able to generalize, further recordings should be taken during a year with no El Niño.

A high number of species vocalizing simultaneously at different frequencies results in high soundscape saturation (Tucker et al. 2014); however, the relationship is
unlikely to be linear. A varied bird song, crossing multiple frequencies, would cause a larger increase in saturation than a simpler insect call, which would only cause a small increase in saturation. Although various soundscape indices have been linked to the number of species vocalizing through the creation of simulated soundscapes (Sueur et al. 2008), future validation work, potentially including automated classification (Acevedo et al. 2009; Aide et al. 2013), will be needed to parameterize relationships between soundscape saturation and species richness of different taxonomic groups.

However, a significant strength of soundscape saturation, relying on the acoustic niche hypothesis (Krause 1987), is that it reflects gross biodiversity without the need to identify species. This is especially useful in forests such as those of Papua New Guinea, where biodiversity research has been limited. In addition to the avifauna, in our recordings from the Adelbert Mountains, the soundscapes were saturated by the vocalizations of amphibians and insects, many of which are likely to be poorly described.

We see the potential of using soundscape recordings as a cost-effective and robust way to quantify the degree to which the vocalizing fauna is intact via the measure of distinct dawn and dusk choruses if similar patterns are found to hold elsewhere in the tropics. The lack of straightforward but robust measures of forest functioning currently represents a barrier to increased financial investment in tropical forest conservation (Burrows 2014). Soundscape sampling may help answer questions about the effectiveness of conservation strategies in tropical forests and provide an affordable way for community forest-conservation programs to document changes in biodiversity through time or between sites. By demonstrating that through a relatively simple analysis of soundscapes, we could distinguish between fine differences in the human impact on tropical forests, we open up a possibility to use soundscape recordings to answer many important questions in ecology and conservation that are impractical to answer with traditional biodiversity monitoring techniques, such as how biodiversity changes with different landscape configurations across large spatial and temporal scales. Answering such questions is crucial to preserving biodiversity in the Anthropocene.

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Supporting Information

Descriptions of land-use zones (Appendix S1), bioacoustic recorder specifications (Appendix S2), methods for analysis of deforestation (Appendix S3), soundscape saturation (Appendix S4), relative importance of environmental and human-impact variables (Appendix S5), relative importance of variables at sites with continuous forest cover (Appendix S6), and detailed information on recording sites (Appendix S7), are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited


