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Measuring sound detection spaces for acoustic animal sampling and monitoring

Kevin Darras^{a,*}, Peter Pütz^b, Fahrurrozi^c, Katja Rembold^d, Teja Tschardt^a

^a Agroecology Group, Department of Agriculture, Grisebachstr. 6, Georg-August University of Göttingen, 37077, Germany

^b Faculty of Economic Sciences, Georg-August University of Göttingen, 37073, Germany

^c Agrobusiness Department, Faculty of Agriculture, University of Jambi, 36361, Indonesia

^d Biodiversity, Macroecology & Conservation Biogeography, Georg-August University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

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ABSTRACT

Sound recordings obtained from passive acoustic monitoring systems are increasingly used to sample animal biodiversity. However, sound recorders sample variable detection spaces, so that data may not be comparable between sampling sites and recording setups.

Focusing on terrestrial systems, we measured understory vegetation, tree structure, sound transmission, ambient sound pressure level, and derived sound detection spaces of 38 plots in lowland rainforest, jungle rubber, and oil palm and rubber plantations, using different combinations of sound frequency (0.05 to 40 kHz) and source height (0 to 5 m).

We show that simple vegetation structure measures poorly predict sound transmission, so that direct sound transmission measurements are indispensable. We depict highly variable sound detection spaces in different land-use types. Finally we estimated species richness of exemplary animal groups and found considerable differences between land-use types on the basis of variable detection space areas alone.

Sound detection spaces respond non-linearly to sound frequency and source height, and they need to be quantified in acoustic surveys to avoid substantial bias in biodiversity estimates between sampling sites. Detection spaces also determine species detection probabilities and allow comparing data between recording setups. We provide guidelines and computer scripts for measuring sound transmission and ambient sound level using consumer audio equipment, and for computing detection spaces. Appreciating the effective sampling area of acoustic recorders closes a gap between acoustic and traditional animal survey methods. Species richness estimates can now be reported for measured sampling areas, and animal population variables such as abundance, density, and activity can be compared at equal areas.

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1. Introduction

Passive acoustic monitoring systems are increasingly prevalent for surveying a wide range of sound-emitting animals: ecologists use these systems to record birds (Celis-Murillo et al., 2009), bats (Bader et al., 2015), amphibians (Aide et al., 2013), insects (Lehmann et al., 2014), terrestrial (Mielke and Zuberbühler, 2013) and marine mammals (Wiggins and Hildebrand, 2007), to determine species richness (Wimmer et al., 2013), to record soundscapes, and to construct general biodiversity indices (Sueur et al., 2014). More complex systems using microphone arrays have been proposed for a wider audience of

biologists to study a variety of other aspects such as anthropogenic noise, species interactions and social dynamics (reviewed in Blumstein et al., 2011). Conservationists recognize the potential of passive acoustic monitoring techniques (Brandes, 2008) and practitioners also increasingly embrace and implement acoustic monitoring programs on large scales (Fristrup, 2009). While challenges in automated signal recognition have been identified (e.g. Swiston and Mennill, 2009), there have been few attempts to standardize the sound recording methodology itself (but see Llusia et al., 2011; Merchant et al., 2015).

Basic biodiversity estimates – such as species richness, activity, abundance and density – are derived from sampling methods that apply to defined areas or volumes, but when sampling sound, it is challenging to measure that space. In essence, biodiversity estimates derived from sound recordings in different sites may not be directly comparable due to site-specific acoustic characteristics: sound travels

* Corresponding author.

E-mail addresses: kdarras@gwdg.de (K. Darras), peter.puetz@mathematik.uni-goettingen.de (P. Pütz), ozykojex@gmail.com (Fahrurrozi), katja.rembold@forst.uni-goettingen.de (K. Rembold), ttschar@gwdg.de (T. Tschardt).

variable distances depending on the frequency, its sound pressure level, the background noise, the location of the sound source and also due to varying topography, climatic conditions and vegetation.

The determinants of sound transmission (or sound attenuation, hereafter “transmission”) are well known. They have been described early for audible sound (Wiley and Richards, 1978) and later also for higher frequencies reaching ultrasounds (Romer and Lewald, 1992). The effect of vegetation has also been specifically addressed (Marten et al., 1977; Marten and Marler, 1977; Aylor, 1972) and reviewed later (Forrest, 1994). In most sound transmission studies, the focus has been on animal communication and rarely on the implications for acoustic biodiversity sampling (though see Hobson et al. (2002) and Patriquin et al. (2003)), a field which has expanded only relatively recently.

The area sampled by acoustic monitoring systems needs to be measured to identify the scale of a particular biodiversity estimate, as basic biodiversity estimates invariably increase with sampled area. Furthermore, it has been recognized that acoustic detectors vary in detection efficacy and range for different bat species (Adams et al., 2012), for aquatic organisms (Huveneers et al., 2015), and also for birds (Rempel et al., 2013). Furthermore birds have different detection probabilities (Sliwinski et al., 2015), but the acoustic sampling area has not been considered yet to tackle these issues. The sampled area also depends on the ambient sound pressure level: distant sounds are more difficult to detect in noisy environments. Relatively early, Morton (1975) calculated distances from the sound source over which sounds would reach the ambient sound level. More recently, a comprehensive analysis of acoustic communication distance determinants was made by Ellinger and Hödl (2003) but it described only one study site and focused on implications for animal communication. We use the term “sound detection space” (hereafter “detection space”), which was introduced later by Llusia et al. (2011), to define the space – in terms of area or volume – sampled by acoustic monitoring systems. Fortunately, the source sound pressure level and frequency – and to a certain degree, the source position – of animal sounds and vocalizations are generally characteristic and measurable for different species, and we assume here that variation between species is higher than within them. Thus, it is possible to compute detection spaces for different species across habitats, but as of today this has not been achieved.

We propose a method to measure sound transmission in various habitat types using consumer audio recording and playback equipment. We challenge the usefulness of our measurements by investigating whether vegetation structure data can predict sound transmission. Then, combining sound transmission values with calibrated ambient sound pressure level measures, we derive detection space areas of different land-use types. Finally, using representative species, we illustrate the impact that variable detection spaces can have on biodiversity measures derived from sound recordings.

2. Materials and methods

2.1. Study region and vegetation structure measurements

The study region is situated in the Batanghari and Sarolangun regencies of the province of Jambi, Sumatra, Indonesia. We recorded sound in 38 plots split into 5 land-use types. Core plots comprised 8 lowland rainforest plots, 8 jungle rubber plots, 8 rubber plantation plots, and 8 mature oil palm plantation (older than 8 years) plots. Six additional young oil palm plantation plots (younger than 4 years) were established to determine sound detection spaces in plantations without closed canopy. Our forest plots are located in an area of disturbed primary lowland rainforest that has been selectively logged in the past. Jungle rubber is an agroforestry system that is minimally managed, consisting of forest and rubber trees. The rubber (*Hevea brasiliensis*, Müll. Arg.) and oil palm (*Elaeis guineensis*, Jacq.) plantations are intensively managed

monocultures. For more detailed information about the study area and the core plot design, see Drescher et al. (2016).

In the 50 × 50 m core plots, all trees with a diameter at breast height (DBH) equal to or higher than 10 cm were counted to derive tree density per hectare, and their DBH was measured to derive total basal area per hectare (Kotowska et al., 2015). Oil palm DBH was measured including the remaining leaf bases which stay attached to the trunk for many years after the leaf is cut, inflating its measure. The trunks in young oil palm plots did not yet reach breast height, therefore their DBH was null; their density was determined by measuring the area of a block containing 49 oil palms (a 7 × 7 block). Tree and mature oil palm height and crown base height were measured using a Vertex measuring device (IV-GS, Haglöf, Långsele, Sweden), and young oil palm height was measured using a meter. Tree height was measured until the tip of the highest branch and oil palm height was measured until the meristem. The crown base height was defined as the height of the lowest branch, or in the case of oil palm the lowest uncut frond. All vascular understory plant individuals (> 1 cm height) growing within five randomly placed 5 × 5 m subplots (3 subplots in young oil palm plots) were counted and their height measured. Understory plant density was expressed as the number of plants per hectare. In core plots, trees were counted and their DBH measured between August and September 2012 (Kotowska et al., 2015); all other plant measurements were carried out between February 2013 and August 2014. In young oil palm plantations, all vegetation structure measurements were done in September 2015.

2.2. Sound transmission measurement

The sound transmission measurements were carried out in March 2014 in the core plots and January 2015 in the young oil palm plots, in good weather (no rain) and windless conditions, when insect noise was not prominent. We ruled out daily micro-climate variation effects by varying measurement times in the focal land-use types (Fig. A1 in Appendix A), although time of day effects on sound transmission are known to be minor (Ellinger and Hödl, 2003). We created a website to help researchers measure sound detection spaces which will be updated with new developments (Darras, 2015).

In the middle of each plot, we attached autonomous sound recorders (“Song meters”: SM2+ and SM2Bat+, default amplifier gain: 48 dB, Wildlife Acoustics Inc., Massachusetts, USA) to a pole at a height of 2 m. The SM2+ recorder was set to a sampling rate of 44.1 kilohertz (kHz) with two acoustic omni-directional microphones for audible sound (SMX-II with Panasonic WM-61 unit), and the SM2Bat+ was set to 192 kHz with two ultrasonic omni-directional microphones for ultrasound (SMX-US with Knowles SPM0404UD5 element). A rope with markings at 1, 2, 4, 8, 16, 32 and 64 m was stretched from the recorder front face to the plot border to position the sound emitters at logarithmically increasing distances. The sound emitters’ polar axes were always at 90° from the microphones’ polar axes, thus ruling out variation in recorded sound level due to the microphone’s polar pattern.

At each marked distance step, we used portable loudspeakers (OnePe DZ-250, Dazumba, Indonesia) and an ultrasound emitter in “chirp” mode (US calibrator Wildlife Acoustics Inc., Massachusetts, USA), to emit audible and ultrasonic test sounds. The audible test sound consisted of a pure tone sequence at 0.5, 2, 4, 8, 12 and 16 kHz, 1 s long at each step, repeated 3 times (Appendix B). The ultrasound test sound was not adjustable and consisted of pure tones at 40 kHz, emitted approximately every 0.25 s for 10 s. The loudspeaker and calibrator were attached to a squeegee with rubber strips to minimize vibration. We emitted test sounds from ground level (10 cm) and then fitted the squeegee onto a telescopic cleaning pole to reach heights of 2 and 5 m. After recording all test sounds from 1 to 64 m (only until 32 m for ultrasound) at all heights, we stretched the rope from the back side of the recorder to the opposite direction and repeated the measurements.

2.3. Ambient sound level measurement

We recorded ambient audible sound and ultrasound in all plots using the same autonomous sound recorders, from the same position. From late June to late July 2014, we sampled audible sound (0–20 kHz) in the core plots over a total period of 12 days; at any day 2 plots in each land-use type (8 plots in total) were recorded simultaneously with SM2+ units set to 44.1 kHz and fitted with two SMX-II microphones. In December 2014, we sampled ultrasound (20–80 kHz) in the core plots over a total period of 8 days; at any day one plot in each land-use type (4 in total) was recorded simultaneously with SM2Bat+ units set to 192 kHz and fitted with two SMX-US microphones. Audible sound and ultrasound from the additional young oil palm plots were sampled in the beginning of July 2014 over 4 days using SM2Bat+ units fitted with one SMX-II and one SMX-US microphone. Ambient audible sound recordings were extracted from 20 min of sound after sunrise on two consecutive days for each plot (three recordings were unusable due to rain). Ambient ultrasound recordings were extracted from 20 min of sound between sunset (around 18:00) and 21:00 for each plot, depending on the timing of rain. We listened to the recordings to identify the sources of sound at different frequency bands.

We produced calibrated sound pressure level measures using the method presented by Merchant et al. (2015) for each recording channel. The base frequency response of the acoustic SMX-II microphone (flat from 50 Hz to 15 kHz) and ultrasonic SMX-US microphones (measured by Wildlife Acoustics Inc. from 20 to 90 kHz), as well as the SM2+ and SM2Bat+ gain and analog-to-digital converter voltage were extracted from the manufacturer's technical documentation to determine the sensitivity of our recording setup. We additionally measured the frequency response of all our microphones relative to each other at each test sound frequency (audible frequencies for SMX-II microphones and 40 kHz for the SMX-US microphone) to account for the differences between individual microphones. Microphone sensitivities in-between the frequencies of the test sounds were interpolated. Finally, we additionally determined the noise floor of our recorder and the directivity of our sound emitters (Appendix C).

2.4. Calculation of sound transmission, ambient sound level, and detection spaces

We calculated sound transmission, ambient sound pressure level and detection space values for each land-use type against all sound frequencies (hereafter “frequency”) and sound source heights (hereafter “height”) to detect trends between land-use types at different frequencies and heights. The audio data were analysed in R 3.10 (R Foundation for Statistical Computing, 2014) with the package *seewave* 1.7.6 (Sueur et al., 2008) and graphs were generated with the package *ggplot2* 1.0.1 (Wickham, 2009). All R scripts and data are available in Appendix D.

For sound transmission measurements, we extracted the sound pressure level from spectrograms with a Hanning window and a window length of 512 ms. We used all pure tones and their background ambient level (1 s from the pure tone for audible frequencies and in-between test sounds for ultrasound tones) at all combinations of frequency, distance, height, direction and plot. We used 2 s for the pure audible tones at their base frequency (± 0.1 Hz) and 2 s for the ultrasound pure tones (40 kHz ± 0.4 Hz) at each combination. Ultrasound test signals were emitted as pure tones with irregular timings, so the amplitude peaks were detected automatically and confirmed manually. We obtained a total of 44,954 sound measures. Clipped signals were detected automatically and rejected. Pure tone sound pressure level values that were <4 dB higher than their corresponding ambient level were rejected too. Estimated distances to the sound source were computed using the Pythagorean Theorem. We used linear regression models to calculate sound transmission: we defined it as the slope of the sound

level linear decay with the logarithm of distance and expressed it in decibel (dB) loss per doubling of distance.

Calibrated ambient sound pressure level was measured from the median frequency spectrum of the ambient sound recordings at a reference level of 20 μ Pa using a modified version of the *meanspec* (R package *seewave*) function (Appendix D) and the methodology proposed by Merchant et al. (2015). The ambient sound level and detection spaces of one young oil palm plot were excluded as we used an uncalibrated microphone.

To derive detection spaces, we determine the sound extinction distance: we defined it as the distance at which the source's sound pressure level reaches the ambient sound pressure level, similarly to Morton (1975). It is also defined as the “communication distance” in research focusing on the implications for animal communication. First, we standardized the loudspeaker's and calibrator's sound pressure level to a reference value of 80 dB at 1 m from the source by subtraction. Then, we obtained the extinction distance at the intersection of the linear sound decay line with the ambient sound level threshold (see Fig. A2 in Appendix A). Thus, the sound extinction distance corresponds to the radius of the detection space, when approximated by a circle, and sound detection spaces were defined as the area of that circle. Data consistency was checked using plots of sound falloff against logarithmic distance to the source at different heights and frequencies at all sites (Appendix E).

2.5. Statistical analysis of sound transmission, sound extinction distance, and vegetation structure

We used an analysis of variance to examine the contribution of land-use type to sound transmission and sound extinction distance. We constructed separate linear mixed-effects models to explain sound transmission and the logarithm of sound extinction distance with land-use type, frequency and height (including all interactions) as predictors, using plot as a random effect. We conducted a stepwise model selection (stepAIC function from R package MASS) for each model to determine the best model.

We also compared statistical models using vegetation structure, plot, and land-use type as independent variables to find the best predictors of sound transmission. Accounting for heteroscedasticity, we constructed separate feasible generalized least squares models for each ecological predictor (plot, land-use, tree height, tree density, basal area, crown base height, understory plant density and height), together with physical variables (height, frequency) to explain sound transmission. A simple model including only the physical variables was also constructed for comparison purposes. Since tree density information would be available whenever trees are measured, we also included tree density as an additional predictor in the basal area, tree height, and crown base height models to improve their predictive power. We used dummy variables for each height and frequency in the feasible generalized least squares models, as they had complex non-linear relationships with sound transmission. We included all two-way interactions between predictors. We conducted a stepwise model selection for each model. The resulting models, each containing its respective ecological predictor, were compared by Akaike's Information Criterion (AIC) scores, which can be seen as a means of comparing models in terms of predictive ability (Konishi and Kitagawa, 2008).

2.6. Simulation of detected species richness based on exemplary detection spaces

We chose four species representing sonant animal taxa (frogs, echolocating bats, cicadas and birds) whose calls were heard in our recordings (recordings in Appendix B) to calculate their detection spaces and then derive the detected species richness of their respective taxa. We used species-specific sound frequency, call sound level, and source height data to compute the species' detection spaces. For the bat and

the bird species, we calculated the call sound level directly from our recordings (method in Appendix C). Birds were represented by the short-tailed babbler (*Malacocincla malaccensis*, Hartlaub), which calls at 71 dB around 3 kHz and is active close to the ground. Echolocating bats were represented by the greater bamboo bat (*Tylonycteris robustula*, Thomas), which is an aerial forager emitting ultrasound mostly around 40 kHz; we determined a call level of 59 dB. For frogs and cicadas, we chose sound source levels of similar species found in the literature. The chosen cicada (family Cicadidae, undetermined species) can be found on tree trunks (approximately 5 m height) and is predominantly heard at 14 kHz (sound recordings in SI). We assumed that it can attain a source sound level of 97 dB, which is the mean sound level of 30 cicada species analysed by Sanborn and Phillips (1995). We chose frog calls (undetermined species) emitted from the ground, and determined a typical sound source level of 100 dB (Penna and Solís, 1998). All call sound levels were expressed at a reference distance of 1 m, relative to 20 μ Pa.

We compared the detected species richness of each animal taxon between land-use systems. To achieve this, we computed the sound extinction distance and the detection space area of each representative species based on its call source level, height and frequency. Second, we translated the representative detection space areas of each taxon to a theoretical detected species richness number using species-area models: we chose the most relevant and best-fitting power-law models as reviewed by Drakare et al. (2006). We chose an amphibian model from the West Indies for the frog (MacLean et al., 1977), a butterfly model from the West Indies for the cicada (Davies and Spencer Smith, 1998), a model for birds of South-East Asia (Brooks et al., 1999) and a model for fruit bats from the Philippines (Heaney, 1991).

We used a linear mixed-effects model with the logarithm of the extinction distance of each species as dependent variable, accounting for heteroscedasticity, to test for differences between forest and the other land-use types with Tukey post-hoc tests (R package *multcomp*). The Tukey post-hoc tests reveal the significance of the expected species richness differences between land-use types, as the extinction distance is only a transformed measure for the detected number of species. For easier comparison and visualization, we visualized the relative detected species richness – which is the detected species richness divided by the mean detected species richness – among all land-use systems.

3. Results

3.1. Vegetation structure proxies for sound transmission

We found that the best predictor of sound transmission was the plot identity, despite the loss of degrees of freedom (Table 1). Land use type also predicted transmission better than any of the simple or combined vegetation structure variables.

Table 1

Comparison of generalized least squares models ($n = 756$) explaining variation in sound transmission, accounting for heteroscedasticity. Akaike Information Criterion scores are shown for the resulting models after stepwise model selection from models including all two-way interactions.

Physical explanatory variables	Ecological explanatory variable	AIC score of LME model	Degrees of freedom
	(None)	2633	21
	Plot	2392	336
	Land use	2496	57
	Tree density	2579	30
	Basal area + tree density	2555	44
Height, frequency	Tree height + tree density	2527	58
	Crown base height + tree density	2522	56
	Understory density	2625	24
	Understory height	2604	30

It was not possible to separate the effects of DBH, tree height, tree crown base height and – to a lesser degree – tree density from the effect of land-use, as the tree variables were characteristic for each land-use. However, we show the relationship between all vegetation structure variables and sound transmission in Figs. A3–5 in Appendix A as there is often significant ($p < 0.05$) positive correlation with tree height, tree density, and crown base height at frequencies above 12 kHz and heights of 2 m, and especially 5 m. Basal area contrasts with the other tree variables, as it does not scale with height in oil palm plantations.

For understory density and height, which show some overlap between land-use types, we found significant correlations with sound transmission (Figs. A3–5 in Appendix A). For instance, understory height is negatively associated with ultrasound transmission at 0 m, indicating that tall vegetation blocks sound for ground-based sources. However understory height has a positive effect at higher source heights (2 and 5 m). Understory density negatively affects frequencies above 12 kHz for sound sources at 5 m, indicating that it absorbs and scatters sound that would otherwise be reflected from the ground.

3.2. Sound transmission patterns

Frequency and height are the main determinants of sound transmission, but land use still has an impact ($p = 0.0065$, see Table A1). The effects of height and frequency were different in each land-use type since their interactions with land-use showed a distinct effect (all $p < 0.05$). Absolute transmission values cannot be compared between frequencies as they depend on our sound source's directivity, which increases with frequency (Fig. A6 in Appendix A), meaning that sound waves become more focused and suffer less loss with distance. However for given frequencies, transmission values can be compared across land-use types and heights.

Generally, the higher the source, the higher the transmission values, but trends vary between land-use types (Fig. 1). At low frequencies (0.5 kHz), plantations have high ground-level sound transmission, probably because they largely lack a scattering leaf-litter layer. In mature rubber and oil palm plantations, at 8 and 12 kHz, sound transmission at medium level (2 m) often surpasses sound transmission at high levels (5 m), presumably because of a wave guide effect (Appendix C).

3.3. Ambient sound pressure levels

In sunrise recordings, forest is generally louder than the other land-use types (Fig. 2). Plantations are noisier at low frequencies (below 0.5 kHz) due to engine noise (motorbikes and cars). At approximately 3.6 kHz, all land-use types exhibit a peak due to bird activity. Plantations and forest experience a peak in ambient sound at 5 kHz due to insect noise. At high audible frequencies (above 10 kHz), forest and jungle rubber have distinctly higher sound levels, with a peak at 15 kHz, due to cicadas (mostly one species).

In night recordings, jungle rubber and forest are distinctly noisier than plantations (up to 20 dB more) but all land-use types follow a similar pattern. There are ambient level peaks from 3 to 6 kHz due to insect noise and at 70 kHz (probably of insect origin). The origins of the peaks in young oil palm plantations at 60 and 70 kHz were unrecognizable. Similarly as in sunrise recordings, low frequencies (50 Hz to 1 kHz) are louder than all other frequencies, which is also due to the higher noise floor of the recorder at low frequencies.

3.4. Detection spaces

Sound extinction distances directly determine sound detection spaces, and the former were mainly determined by sound source frequency and height (see interactive plot), but land-use type still had a minor effect (Table A2). Detection spaces are smallest in forest sites, and generally increase with sound source heights (Fig. 3). Compared

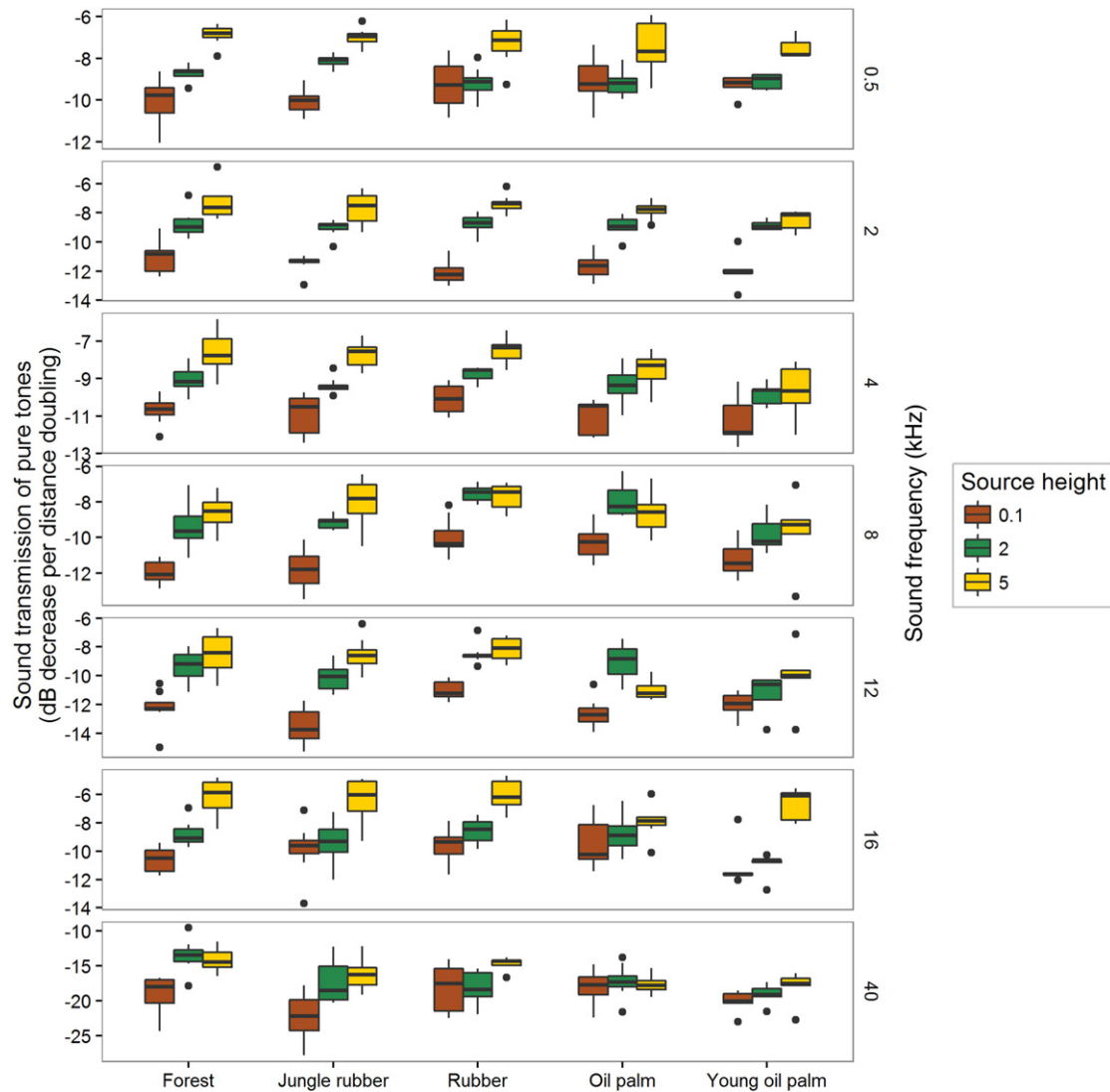


Fig. 1. Boxplots of sound transmission values for different sound frequencies, source heights, and land-use systems.

with forest and jungle rubber, plantations have greater detection spaces at audible and ultrasound frequencies, except between 4 and 6 kHz, where their ambient sound level is high (Fig. 2). However, detection spaces in oil palm are distinctly smaller than the other plantations at 5 m, as the sound source would often be masked by the fronds. Only for sound sources at a height of 2 m at 40 kHz (night time) and also at 50 Hz (at sunrise) do forest habitats have markedly bigger detection spaces than the other land-use types. Forest detection spaces reach their minima at 15 and 3.6 kHz, where their ambient sound levels are high.

3.5. Detected species richness

Fig. 4 demonstrates that depending on the strength of the call, the sound frequency used by animals, and the stratum in which they vocalize, different trends in detected species richness could be observed on the basis of sampling area alone. We depict p-values under the assumption that there is no difference between the relative species richness of forest and the respective land-use. Generally, forest sites have the lowest relative detected species richness except for echolocating bats. Rubber plantations consistently reached relatively high values.

4. Discussion

4.1. The need to measure sound transmission and detection spaces directly

No simple vegetation structure proxy can be used to determine the sound transmission of a particular habitat or location. Alternatively, more complex combinations of vegetation structure measures could be used to predict sound transmission more accurately (Embleton, 1963). However, any such calculations would involve more effort than measuring sound transmission directly. Furthermore, we already tested some combined tree variables (e.g. DBH with tree density data), but none of these were satisfying predictors. It is possible that understory measures, which were measured over the course of more than one year, did not exactly represent the plot's understory condition at the time of the sound measurements, but they were still representative of each land-use type.

Land-use type does not predict sound transmission precisely enough either. Similarly, earlier work on sound transmission (Marten and Marler, 1977; Marten et al., 1977) suggested that habitat affects sound transmission only slightly. Climatic conditions, which also affect transmission, are typical for each land-use type but they differ only little between land-use types (Drescher et al., 2016). Sound transmission differences would have been greater if we had compared open and

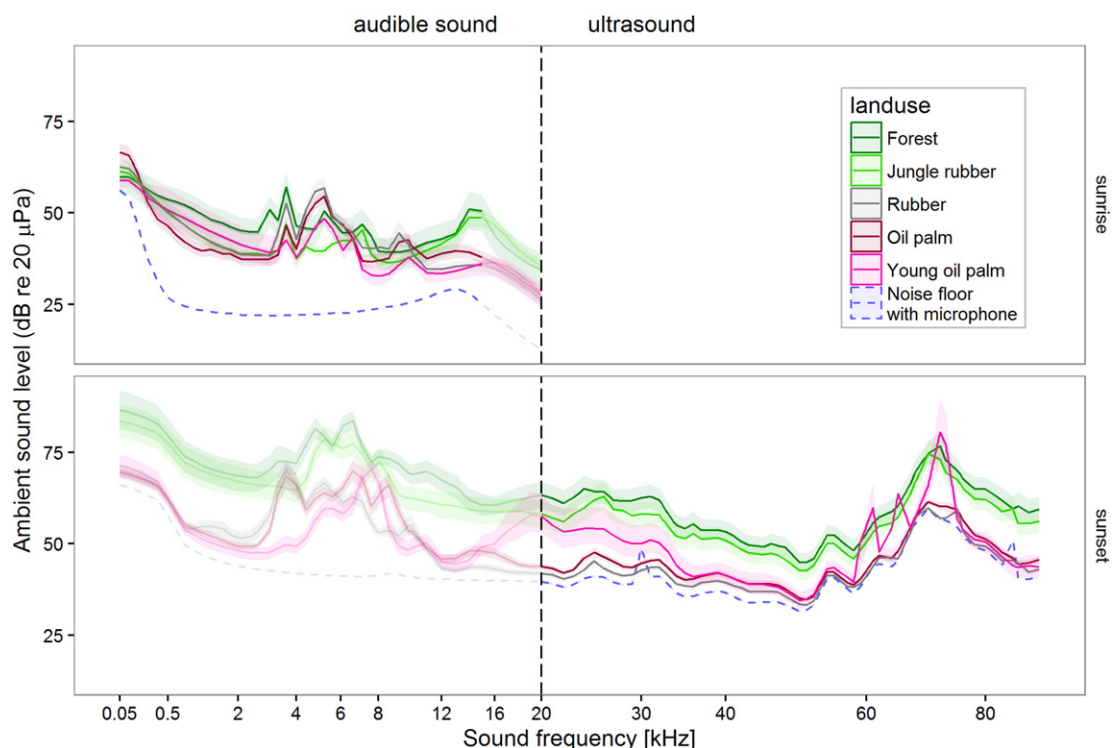


Fig. 2. Means of the ambient sound median frequency spectrum (window length: 512) for different land-use systems. Acoustic and ultrasound levels were respectively extracted from 20 min of dawn recordings on two consecutive days and 20 min of night recordings. Error bands represent standard errors of the mean.

wooded systems – young oil palm plantations did not have a closed canopy but the palm fronds were as high as 5 m.

Presumably, the large unexplained variation in sound transmission within land-use types was due to site-specific differences in plant composition, leaf morphology, and topography. Indeed, plot-level data

predicted sound transmission best, solidly supporting our recommendation to measure sound transmission directly in each sampling site. The underlying sources of variation leading to the observed patterns in sound transmission are manifold. Our study was not designed to address these, but they are discussed elsewhere (Appendix C).

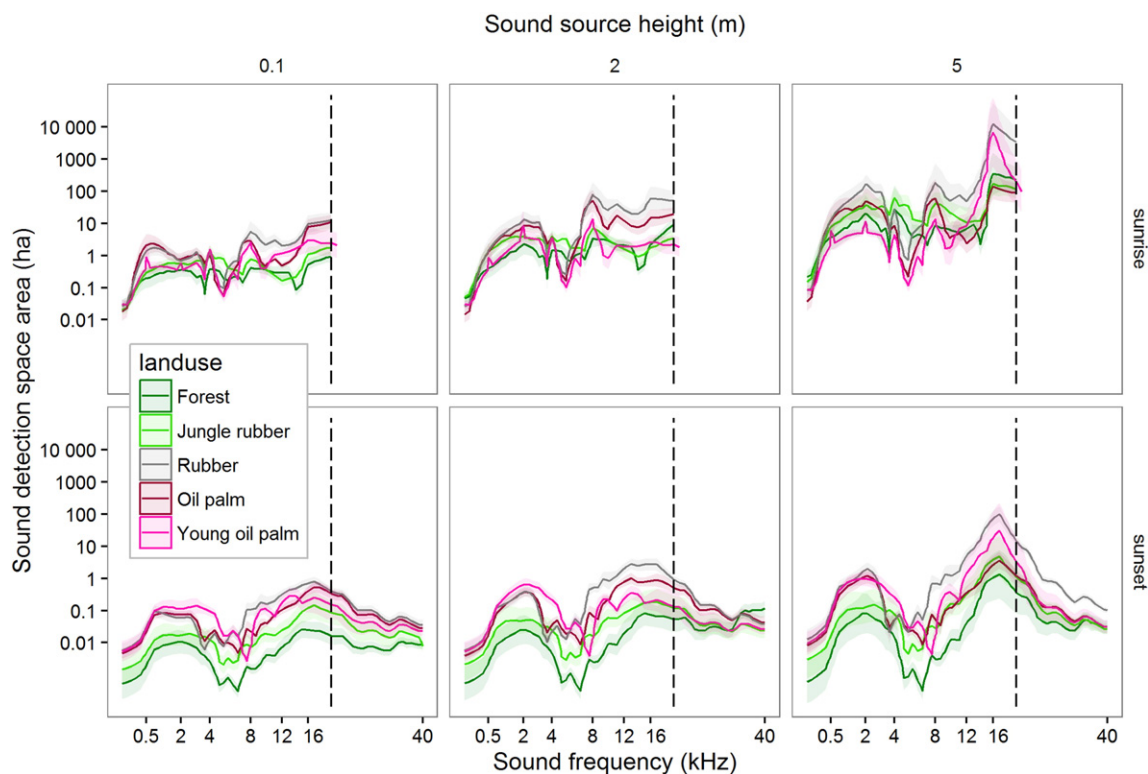


Fig. 3. Geometric mean of sound detection space areas for different frequencies and sound source heights in different land-use types, error bands represent standard errors of the mean. Our sound source had increasing directivity with frequency and a source level of 80 dB. See the iPlot for an interactive version.

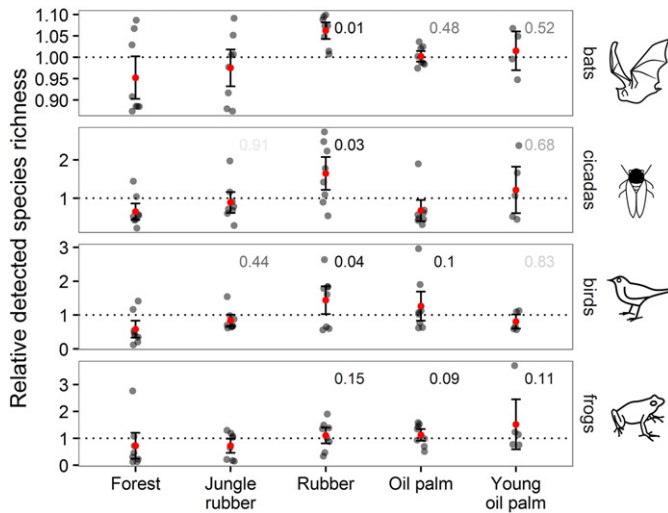


Fig. 4. Detected species richness relative to the mean detected species richness across all land-use types. Detected richness describes the number of species that would be found based on the detection space area alone. Mean richness for each land-use type is indicated by red points with standard error of the mean error bars. p-Values (rounded to 2 decimals) under the hypothesis of equal species richness to the forest are depicted and derived from a post-hoc test based on a linear mixed-effects model of sound extinction distance with plot as random effect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. Variation in ambient sound

Ambient sound levels varied considerably with frequency, but they were also distinct between land-use types (Fig. 2). They are variable throughout the day and across seasons too, but minor day-to-day variation was averaged out with our replicates. Similarly, Ellinger and Hödl (2003) show that ambient noise varies tremendously with the time of the day and the frequency. Thus to fully account for the variability in ambient sound level, multiple time periods should be sampled. However, here we refrained from analysing temporal patterns and focused on dawn levels corresponding to peak bird calling times, and nightly ultrasound levels corresponding to bat and frog calling times. Correspondingly, we advise to match ambient sound recordings with the typical daily activity time of the monitored animals, while also measuring ambient sound during the different sampling seasons. Furthermore, Ellinger and Hödl (2003) emphasized that ambient noise affects communication distances – thus detection spaces – more than sound transmission. We confirm their findings because the differences in ambient sound level between land-use types were more pronounced than those in sound transmission.

4.3. Variation in detection spaces

We saw that detection space areas also vary tremendously: analogously to ambient sound level, detection spaces are affected by land-use (Table A2), as well as frequency and time of the day (Fig. 2), but also height (Fig. 3), like Ellinger and Hödl (2003) showed. Thus, the vocalizing organism is an important determinant due to its choice of stratum within the vegetation. Moreover, the sound level of its vocalization affects detection spaces greatly as they increase with the square of the sound extinction distance. In addition, the latter increase exponentially with higher transmission values, which might result from calls that are lower-pitched or more directive (Patricelli et al., 2007). Variation in detection spaces becomes even higher when considering species with multiple songs in their repertoires, which might be emitted from different heights. Likewise, complex songs spanning a wide frequency range would not have a unique sound detection space value but rather different detection spaces at each combination of frequency and source level.

Hence, out of simplicity and feasibility, we recommend referring to the maximal sound detection space area attained by animals at their highest sound level with their best-transmitting call frequency.

4.4. Implications for ecoacoustic studies

Here we derived theoretical species richness values for different exemplary animal groups. We demonstrated how the differences in sound detection space areas would translate into flawed estimates of species richness between land-use types, even though they are relatively similar in our case (all systems contain trees providing a more or less closed canopy). Our results are different for each animal group and underline the multitude of factors which determine the detection space of the species: mainly the sound source amplitude, the stratum it vocalizes in, the sound frequency it uses, the background noise it experiences, and the land-use in which it is emitting sound. Fortunately, our results allow quantifying the sampling area in different sampling sites. We elaborate on technical recommendations separately (Appendix C).

Methodological studies are particularly affected by sound detection space theory. It has been shown previously that acoustic recorders differ in their detection efficacy for different animal groups (Adams et al., 2012; Huveneers et al., 2015; Rempel et al., 2013). Indeed, quantifying the detection spaces of these recorders would allow us to compare data from different recording systems and sites. It should be noted that although their ranges would not simply depend on the polar pattern and sensitivity of the microphones used but also on the recorder noise floor and microphone signal-to-noise ratio, and these specifications are implicitly taken into account when measuring detection spaces. The different detection areas sampled by different survey methods also have not been taken into account in several studies reporting the efficacy of point counts versus acoustic recordings (Acevedo and Villanueva-Rivera, 2006; Alquezar and Machado, 2015; Celis-Murillo et al., 2012): clearly, survey methods with larger detection spaces should yield more detections. Similarly, quantifying detection spaces of single species has high relevance for calculating species detection probability and their measured occurrence. It was already suggested by de Solla et al. (2005) on the example of anuran surveys, that species detectability is driven by specific calling strategies. Indeed detection spaces, when multiplicatively coupled with calling frequencies and population densities – which are respectively probabilities of calling and presence – should be the main determinants of acoustic detection probability. Detection spaces thus offer an alternative method for calculating species occupancy models.

Biodiversity surveys would generally also benefit from quantifying detection spaces. In our study, we observed high correlations between vegetation structure and ultrasound transmission, suggesting that habitats with contrasting vegetation will affect bat detection differently. Indeed, it was shown that vegetation measures correlate with bat activity (Ford et al., 2005), and they have been taken into account in occupancy models recently (Bader et al., 2015). Although it was recognized early that ultrasound transmission differs across habitat types (Patriquin et al., 2003), and it has been observed to affect sampling of bats directly (Kalcounis et al., 1999), such considerations are not systematically taken into account (see for example Frey-Ehrenbold et al., 2013; Jung et al., 2012; Newson et al., 2015). We argue that instead of measuring vegetation variables, direct quantification of detection spaces would be more useful. Along the same line, variable detection spaces affect the results obtained from sampling birds in different habitat types (e.g. Wimmer et al., 2013; Sebastián-González et al., 2015), and they could even influence acoustic diversity indices in relation to vegetation structure (Pekin et al., 2012), since sites with higher sound transmission would have a higher chance of yielding a higher acoustic diversity.

Interestingly, call transmission measurements have been used in a few cases for calculating detection ranges of single cryptic bird species (Lambert and McDonald, 2014) and temperate song birds (Furnas and Callas, 2015), although in the latter case it is unknown how much

they varied between species. The authors could make valid comparisons of abundances between habitats on the basis of an identical acoustic sampling area, taking into account the bird call's source level and height.

4.5. Applications for acoustic animal sampling

Obtaining species richness estimates from acoustic data that are comparable between sampling sites is challenging, as the relationship between area and species richness is not linear. Moreover, each land-use type actually follows its own species-area relationship. On one hand, detection spaces can be larger in some habitats, but they can have shallower species-area curves (e.g. in plantations for birds), which counteract the depicted differences in relative richness. On the other hand, habitats with greater detection spaces do not necessarily have shallower species-area curves (e.g. forest for bats), so the effect can be reversed and is entirely dependent on the organism and its stratum. Hence, calculating expected species richness for a common reference area requires considerable knowledge; comprehensive studies are needed to estimate accurate species-area model parameters and derive absolute species numbers.

Alternative methods still need to be devised to compare species richness without bias in the field of ecoacoustics, especially because richness is the measure of choice for appreciating biodiversity and its conservation value. As we alluded here (Fig. 4), for a simple correction, relative detected species richness could be used as a multiplicative term to correct the total species numbers. However, the species richness numbers we derived for the different taxa were based on single species' detection spaces. Otherwise, when transmission values are known for sampling sites, noise could be artificially added to sound recordings to cap the detection spaces to a common, equal area. However, all approaches would require individual calculations for each species, since call sound levels vary considerably, so that the task is daunting for any-one sampling entire communities. While detection spaces of some species might be used to represent others, some of the variation would be swept under the rug. Overall, easy solutions are not available yet for quantifying detection spaces of each species in entire animal communities, but our study reveals the complexity of acoustic detection space matters and cautions strongly against ignoring them.

Estimating distances to each animal call is an alternative, tempting, and simple method since all detections below a certain threshold could be filtered to yield a dataset that enables unbiased species richness comparisons while avoiding dealing with the complex, multiple factors affecting detection spaces. Listeners could estimate distances to each animal call in the sound recordings, although the uncertainty might be substantial (Alldredge et al., 2007). Additionally including sound recordings of test sounds from increasing distances could allow them to appreciate the sound transmission and assist them to estimate call distance. However, it is unknown how accurate human distance estimates from unattended sound recordings would be. Provided animal sound source levels are known, measuring the sound level, and ideally the directivity of animal calls in sound recordings and gauging them with measured transmission values could yield more trustworthy extinction distance estimates and detection spaces.

Other animal population variables like abundance and activity are more straightforward to compare. For instance in one sampling site, animal calling activity and abundance probably increase linearly with the sampling area and thus become quantifiable with known detection space areas. With these measures, comparison at a common denominator area is easier, since we only need to divide them by the sampled area or interpolate to the lowest sampled area. In that sense, detection spaces can be used further to calculate population densities too, simply by dividing the number of detections by the sampled area, addressing a shortcoming of acoustic sampling systems underlined by Acevedo and Villanueva-Rivera (2006). With bird recordings, listeners can even distinguish between individuals and estimate true abundances by using known call repetition rates and localizing the sound source in stereo

recordings. Previously, to calculate population densities with acoustic data, uncalibrated microphone arrays were used (Dawson and Efford, 2009), making the analysis and survey setup inherently more complicated. In contrast in marine systems, the theory behind animal density estimation using acoustic data is more advanced and has been reviewed by Marques et al. (2013), although the necessity for measuring detection spaces also prevails.

To some degree, the challenges we underlined for acoustic monitoring also apply to traditional survey methods like point counts. We argue that gauging sound detection spaces allows animal ecologists to obtain comparable data from acoustic surveys as they would obtain from traditional surveys, thereby closing a knowledge gap between these two methods. Although we have exposed the complexity of measuring sound detection spaces and accounting for them in animal acoustic biodiversity surveys, we believe this is a necessary evil to take advantage of the compelling potential offered by passive acoustic monitoring systems as a tool for conservation science.

Glossary

Sound transmission: coefficient of the linear decay of the sound pressure level with the logarithm of distance to the source level.

Sound extinction distance: the distance at which a source's sound pressure level reaches the ambient sound pressure level.

Ambient sound level: Sound pressure level of all surrounding sound, usually sampled with omnidirectional microphones.

Species-area curves: Curves describing the relationship between total number of species and the area of the sampled area, both of which might be log-transformed.

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Appendix A–E. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.06.021>.

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