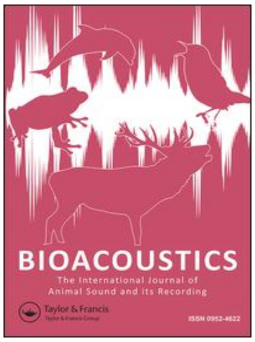


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# Slope does not affect autonomous recorder detection shape: considerations for acoustic monitoring in forested landscapes

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**ABSTRACT**

To date, there are no published guidelines on how to optimally install recorders on sloped terrain, although slope could potentially affect a recorder's detection space. This study experimentally investigated the effect of microphone orientation in relation to slope of recorders from two cost classes. We installed four recorders at each plot centre (n = 16), oriented either parallel or perpendicular to the slope. We played standard tones of 1–11 kHz at distances of 10, 20, 40 and 80 m from the recorders. Our two response variables were the presence/absence of each tone (coarse spatial scale) and predicted sound extinction distance (fine spatial scale), which were tested for effects of microphone orientation and sound source direction (SSD). We observed a significant effect of microphone orientation on extinction distance when recorders were perpendicular to the slope at the finer spatial scale as an interaction with SSD, indicating that microphones are biased towards the direction they face. Despite the advertised directionality of most recorder microphones, detection space is not circular. This trend was observed across all frequencies, for both high- and low-cost recorders. Microphone orientation in relation to slope is not an important methodological consideration, instead dominant factors such as frequency and prevailing wind direction drive detection space shape.

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**KEYWORDS**
Acoustic monitoring; autonomous recording unit (ARU); detection probability; recorder detection space; slope; sound transmission

## 1. Introduction

Acoustic recordings provide permanent, temporally high-resolution environmental records and have been demonstrated as a powerful tool for sampling sonant species, particularly birds (Gasc et al. 2017; Shonfield and Bayne 2017). As use increases for both ecoacoustic and bioacoustic monitoring, the necessity to standardise sampling methodology and account for differences in recorder detection space – the 360° range in which sound transmission from a sound source to a recorder above ambient noise levels is successful – becomes more important. Accurate knowledge of recorder detection space is crucial for spatially valid study designs. It is also necessary to control for biases inherent to the sampling method – particularly when recording species that vocalise at different frequencies and amplitudes – which would allow researchers to standardise variations in detection per site, yielding more accurate biodiversity estimates (Darras et al. 2016).

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Supplemental data for this article can be accessed here.

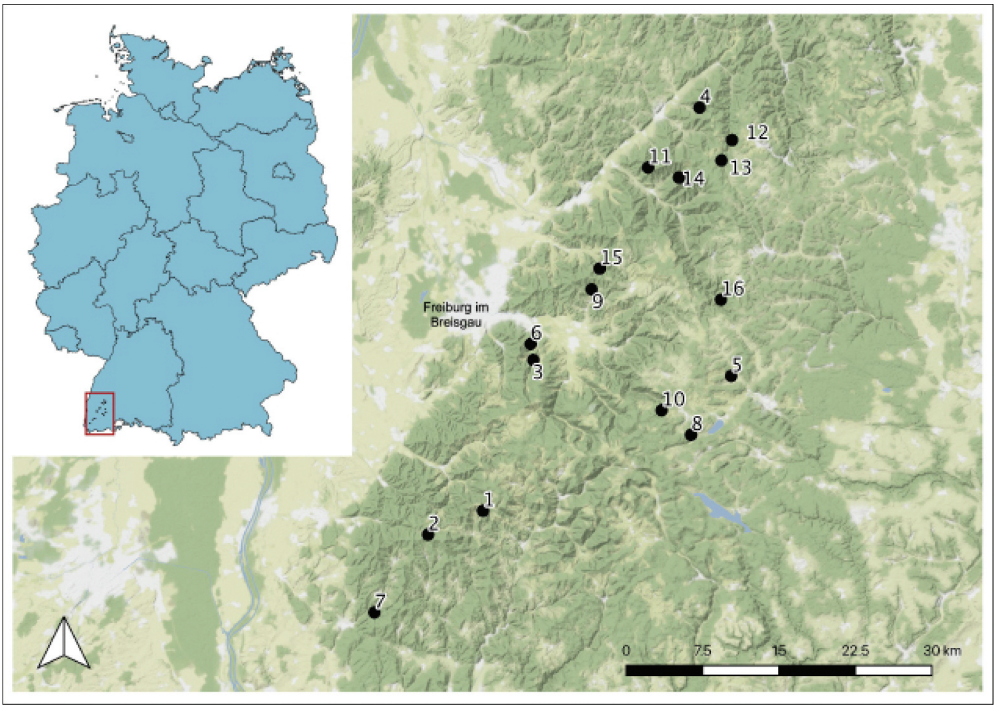


**Figure 1.** Final plot selection for acoustic tests conducted in August 2018 on slopes between 20 and 30º. Plots range in elevation from 500-1250 m a.s.l., and are located in the southern Black Forest, Germany.

Sound transmission in forest ecosystems is a long-studied subject. The inverse square law predicts that due to spherical spreading, sound pressure levels (SPLs) will halve with each doubling of distance a sound wave travels in a frictionless environment. In addition to the effect of distance, in a forest, sound waves are subject to the effect of ground attenuation at low frequencies (<1 kHz), scattering, refraction and absorption by trunks and branches (<2 kHz) and foliage (>5 kHz) (Embleton 1963; Aylor 1972; Price et al. 1988), and interactions between these effects are complex, not simply additive (Huisman

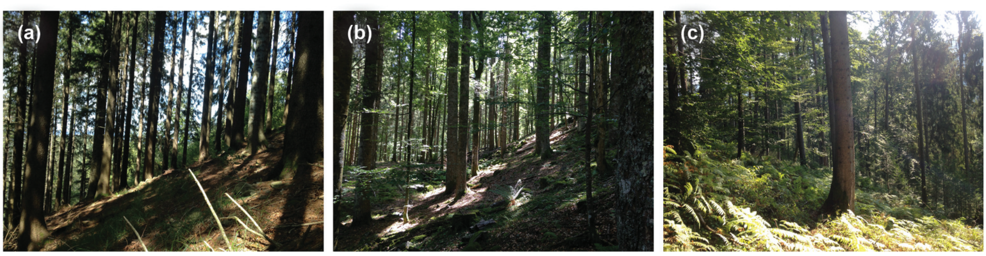


**Figure 2.** Understory of plots: examples of a (a) minimally dense understory with only small rocks and ground litter, visibility ~60-80 m; (b) moderately dense understory plot, which was typical of most sites, visibility 40-60 m; (c) maximally dense understory with presence of slight regeneration, ferns, sedges and grasses, visibility 20-40 m.

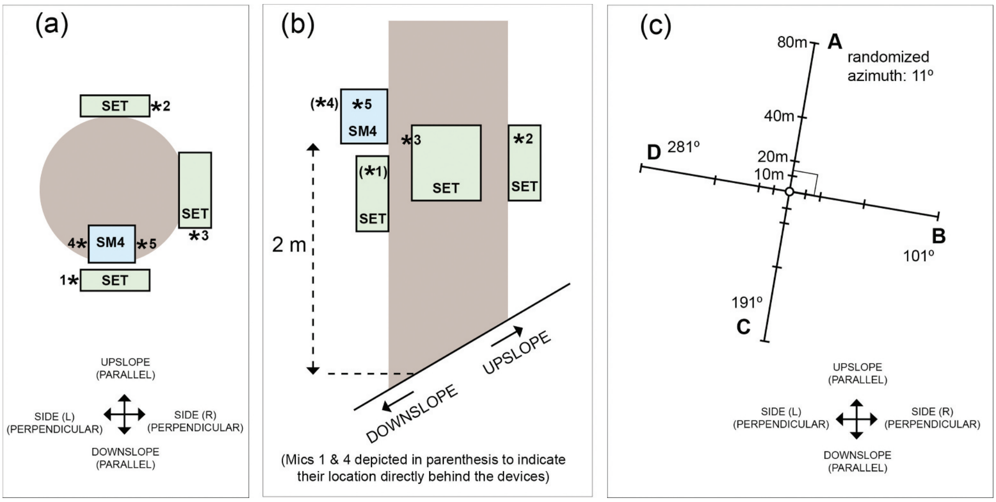


**Figure 3.** Panes depict (a) an aerial view of four recorders on tree and (b) a side view of the same arrangement. Microphones, located on the side of the recorders' housing, are indicated by numbered stars and face either parallel or perpendicular to the slope. Figure (c) depicts an aerial example of Transects A-D conducted from a plot center, where the recorders were installed. SET and SM4 indicate the two different recorder models used for this study.

and Attenborough 1991). Atmospheric conditions such as temperature, humidity, wind, and turbulence further affect sound transmission from source to receiver and subject even a pure tone to constant flux (Ingård 1953).

The general consensus among studies in tropical to boreal forests is that recorders have a presumed circular detection space (Darras et al. 2016; Yip et al. 2017a, 2017b) and that they capture vocalisations well within the first 40–75 m (Hobson et al. 2002; Celis-Murillo et al. 2012; Vold et al. 2017). They are most advantageous at detecting vocalisations within the first 50 m, and although detection distances vary greatly, detection distances can reach a maximum of 150 m and tend to decrease with vegetation density (Venier et al. 2012; Rempel et al. 2013; Furnas and Callas 2015; Van Wilgenburg et al. 2017; Darras et al. 2018). Additional considerations affecting the detection distance in a forest include ambient SPLs, and qualities of the sound source such as volume, directionality, frequency and distance from the receiver (Padgham 2004; Darras et al. 2016). Height is also an important factor: signals were found to travel farther with higher source height and receiver (microphone) height (Ingård 1953; Marten and Marler 1977; Ellinger and Hödl 2003; Padgham 2004; Darras et al. 2016). Variations between recorder types also affect signal detection (Yip et al. 2017b), through differences in microphone sensitivity, signal-to-noise ratio (SNR), recorder self-noise/noise floor (Darras et al. 2018), directionality and frequency sensitivity (Rempel et al. 2013), weatherproof housing and location of microphone on a recorder.

Taken together, the factors influencing detection space are myriad and thus are highly variable; however, an additional factor which may further affect detection space is terrain slope. Evidence of 'sound shadows' (Morton 1975), height effects, ground attenuation and scattering from vegetation together illustrate how signal detection is impeded by

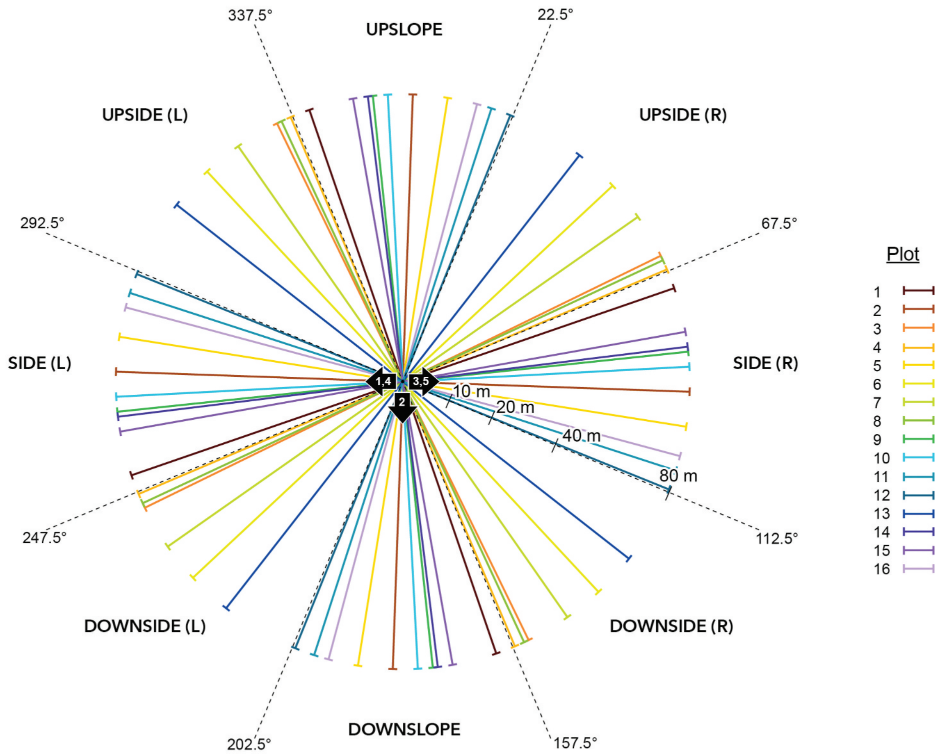


**Figure 4.** Distribution of transects occurring in 16 plots. Dotted lines indicate divisions of eight categorical directions from which the sound sources originated in relation to the transect center, corrected for aspect (aspect = 180°). The numbers inside the black arrows represent the five microphones, and the black arrows represent the direction microphones faced in relation to the slope.

a signal's interaction with the ground and surrounding vegetation. Changing the angle of the ground (i.e. slope) changes the angle at which these interactions occur, potentially affecting signal transmission and thus the presumed circular detection space of acoustic recorders.

At present, it is standard to install recorders 1.5–2 m above the ground but there is no best practice for how to orient a recorder in relation to slope. We found mention of slope-related signal detection in two publications: Hunter (1989) observed that of 21 passerine species in the Himalayas, 77% of observed vocalisations faced uphill, providing slight evidence that recording from above the sound source may be beneficial. Darras et al. (2018) recommends always placing microphones parallel to the ground, meaning on flat ground they would be horizontal and on a slope they would be rotated slightly so that the top and bottom edges of the recorder remain parallel to the ground. It is more practical, however, that researchers install their recorders directly to tree trunks without adjusting the recorder's angle with respect to the ground. Recorders are typically affixed to a tree with a strap or rope, making anything other than a horizontal installation logistically difficult. Further, this recommendation was made on the assumption that detection spaces are circular and recording parallel to the ground is always optimal, while the

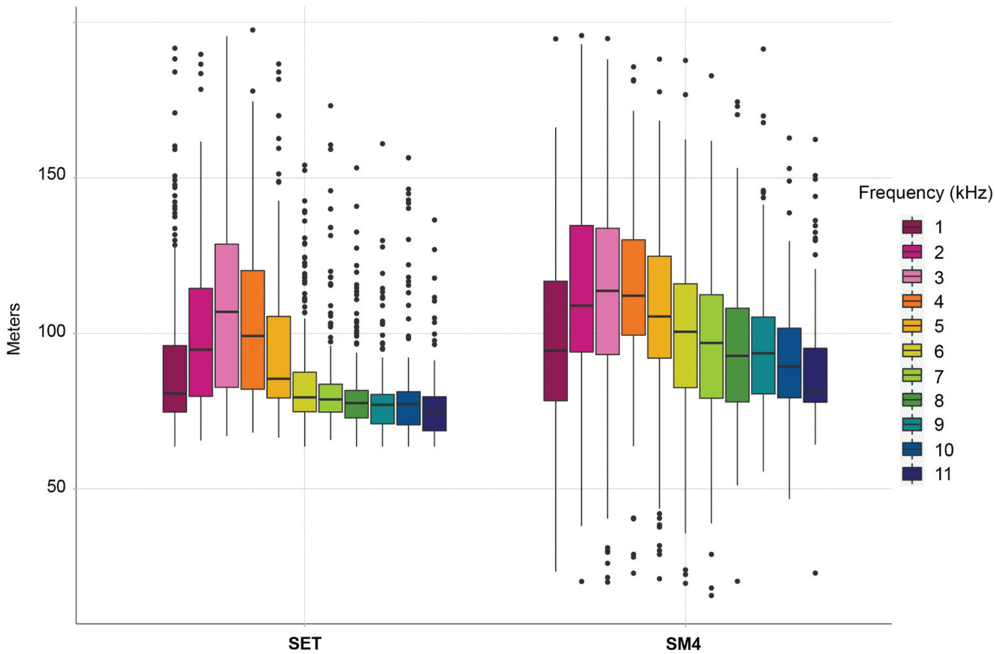


**Figure 5.** Extinction distance by device, Lunilettronic Soundscape Explorer (SET) and Wildlife Acoustics SM4.

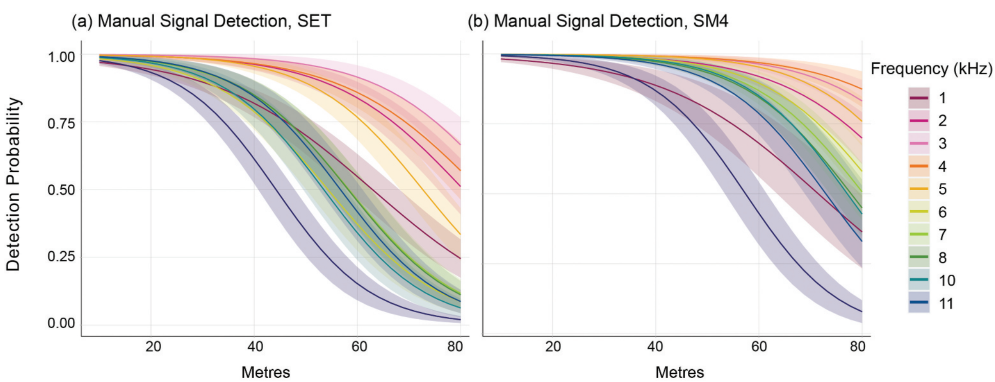


**Figure 6.** Probability of manual signal detection for SET and SM4 devices. Detection probability per device was almost identical for the three microphone orientations to the slope (Side (L), Side (R) and Downslope), thus only Side (R) is displayed here (see Appendix 4 for all microphone orientations).

presence of a slope may produce effects that undermine both of these assumptions. Taken together, no empirical work exists testing sound transmission over sloped terrain; thus, we sought to investigate how horizontal microphone installation, either parallel or perpendicular to the slope, may interact with other drivers affecting detection space.

Given the ecological importance of mountainous regions (e.g., Perrigo, Hoorn and Antonelli 2020) and increasing use of acoustic recorders for biodiversity monitoring – particularly in mountainous areas where access is difficult, as data can be collected

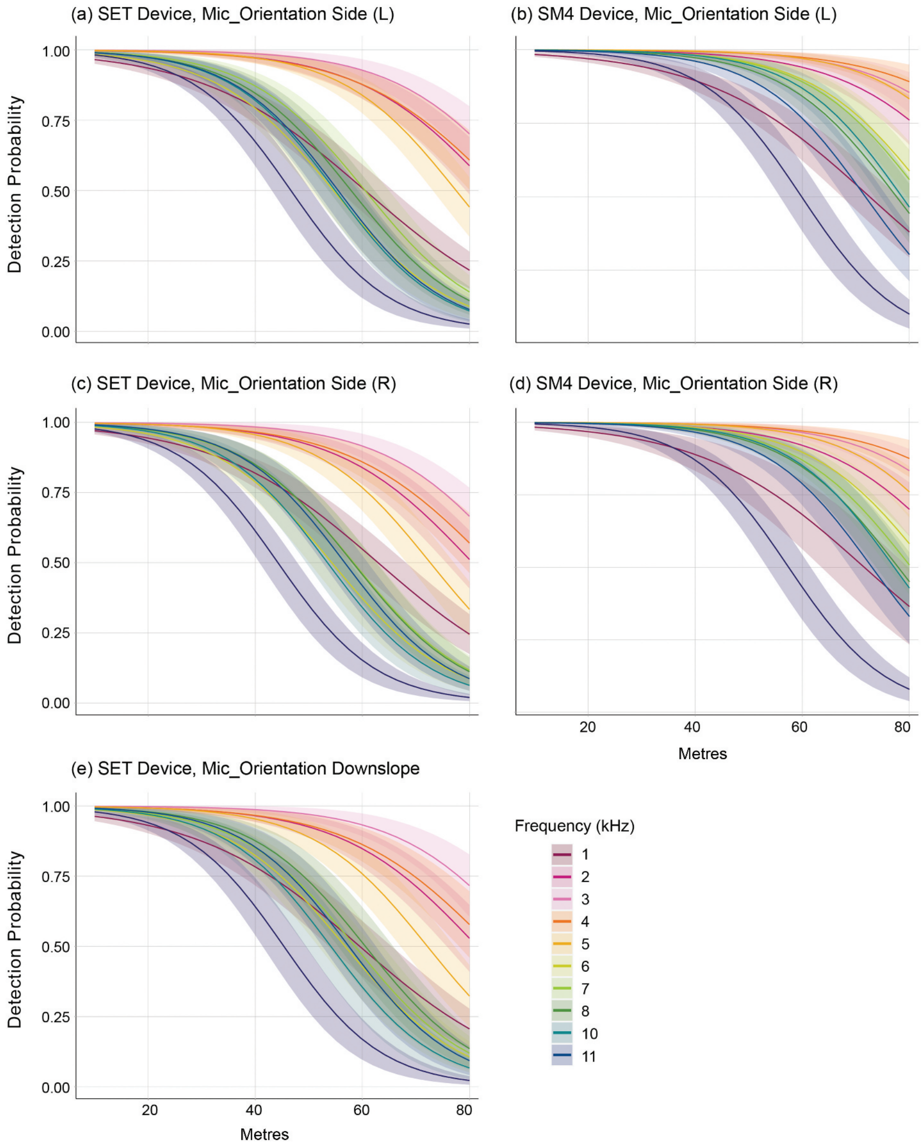


**Figure 7.** Probability of manual signal detection for SET and SM4 devices by microphone orientation.

automatically, stored safely and retrieved when conditions permit – we posit that filling the above-mentioned knowledge gap is an important methodological step for the standardisation of research in this field. We expect a range of factors in addition to slope to influence signal detection; thus, the aims of this research are to (1) test the effect of microphone orientation in relation to slope on detection space and in doing so (2) highlight the relative influence of additional factors (e.g., microphone quality indicated by device type, sound source direction) that determine the 360° shape of detection space. Given the known variability between different ARU devices (Yip et al. 2017b), we tested recorder models from two cost-classes to better generalise any identifiable slope-related

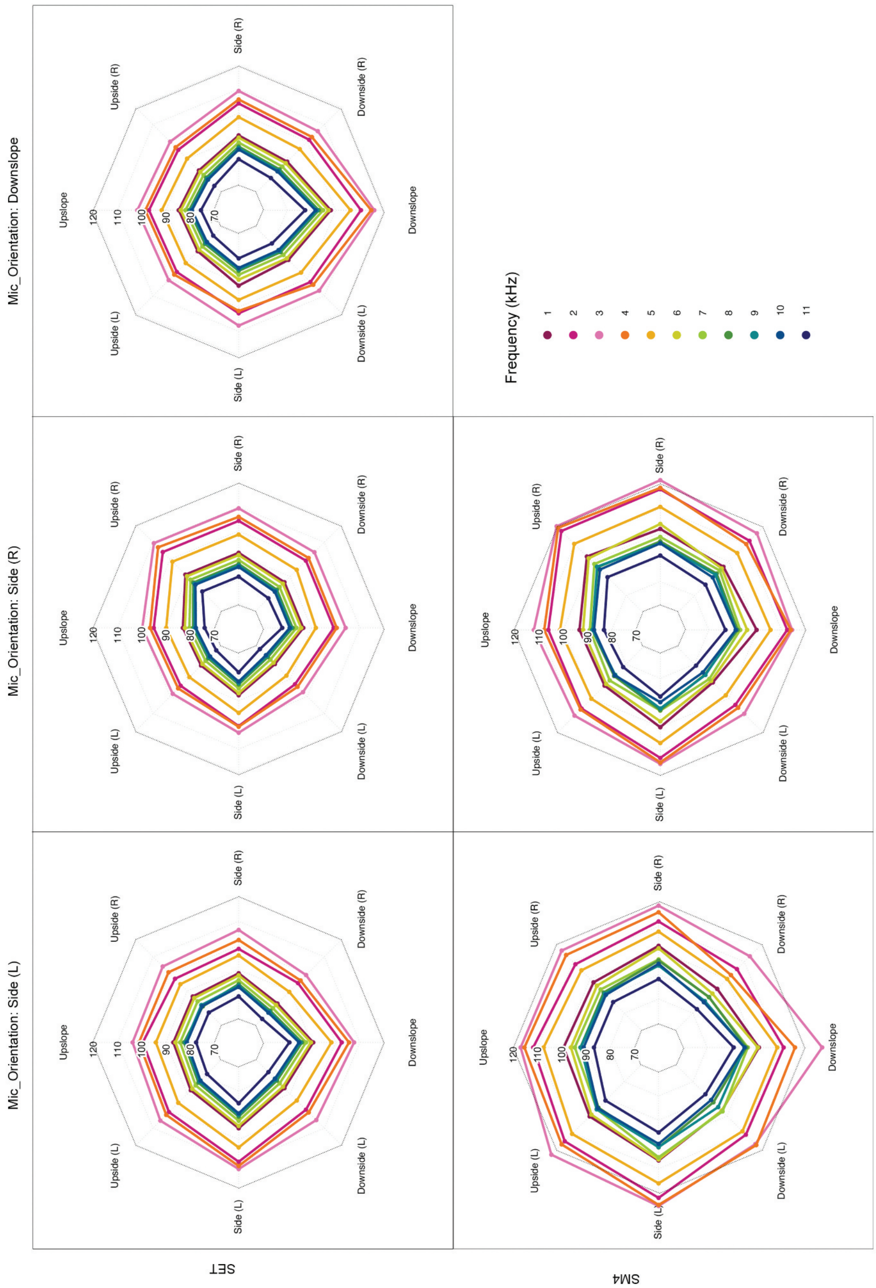


**Figure 8.** Mean predicted extinction distances from best-performing Extinction Distance model (M15), by device and microphone orientation. The extinction distance for each tone (1-11 kHz) originating from a given SSD is depicted separately in each graph. Many confidence intervals overlap, but for plot clarity they are located separately in Appendix 5.

patterns. We investigated individual frequency response to microphone orientation in relation to slope, device type, sound source direction, plot structure and atmospheric

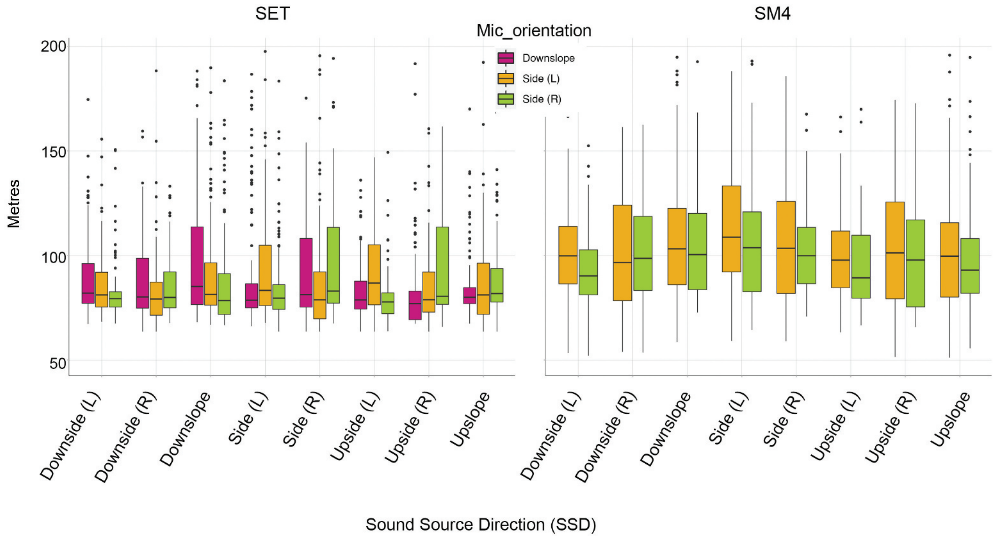


**Figure 9.** Extinction distances depicting the interaction between microphone orientation and sound source direction, by device.

variables to understand the range of interacting factors affecting detection space shape and to assess their relative effects on our dependent variables, signal detection probability and sound extinction distance.

## 2. Materials and methods

### 2.1. Study area

Our study area contains 135 one-hectare plots located in the southern Black Forest, Germany, a temperate mixed montane forest dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) (see Storch et al. 2019 for details). The plots have mostly closed canopy and are comprised of mature stands >65 yrs. Fifty-four plots were selected by an average slope ≥20°, and further subset by removing plots with the presence of topographic or vegetative characteristics that would bias acoustic tests. Exclusion criteria included the presence of cliffs, large boulders, high tree mortality (large gaps) or high conifer regeneration (high understory vegetation density), resulting in 32 plots. The selection was further narrowed by the number of trees present to control for tree density; 50% of the plots around the median number of trees were selected. The final selection resulted in 16 plots with slopes of 20–30° with mostly open understories of sparsely distributed young trees and shrubbery (Figures 1 and 2).

Fieldwork took place from 18.08.18 to 22.08.18. We conducted playback tests in August after foliation had occurred at all elevations. The presence of animal vocalisations in a recording could mask the test signal, effectively decreasing the detection distance for that test. Hence, testing in late summer, when birds are least vocally active, minimised the probability of simultaneously recording birdsong. Tests were not conducted in rainy or windy conditions. Plot slope and aspect were recorded on site at the plot centre. Additional variables were available from a 2017 inventory: mean diameter at breast height (DBH), basal area and number of trees per plot were calculated for all living trees >7 cm DBH. Plot means for elevation, coarse woody debris, Normalized Difference Vegetation Index, and Terrain Ruggedness Index were also included in data exploration (Storch et al. 2019).

## 2.2. Recorder setup

Four devices were used in this study: three LUNILETTRONIK Soundscape Explorer Terrestrial prototypes (hereafter SETs) (Lunilettronik Cooperativa, Fivizzano, Italy) and one Wildlife Acoustics Song Meter SM4 (hereafter SM4) (Wildlife Acoustics, Inc., Massachusetts, USA). The SETs incorporate one external omnidirectional microphone (EMY-63 M/P) on the left side of the device with a sensitivity of −38 ± 3 dB and an SNR >60 dB. The SET prototypes are no longer available, but at the time of purchase cost EU €130. The SM4 has dual-channel recording capability with two omnidirectional microphones on either side of the housing, with a sensitivity of −35 ± 4 dB and SNR ~80 dB. At the time of writing, the SM4 costs US$850.

We installed the devices 2 m high on the same tree at the plot centre, with microphones facing either parallel or perpendicular to the slope (Figure 3a-b). Tree selection was made at the plot centre, meeting the criteria of 40–50 cm diameter at breast height (DBH), as too small a tree would not accommodate all devices at the same height, and too large a tree would create a sound shadow. Due to the limited availability of devices (one SM4, three SETs), the SETs were faced towards directions intended to maximise detection distance: to either side perpendicular to the slope and directly downslope (parallel). The placement of SETs was randomly assigned per plot to account for any variability between recorders.

## 2.3. Audio transects

We conducted four transects (A-D) per plot. Transect A direction was determined by a randomised azimuth (randomly generated number from 1 to 360 per plot), and subsequent Transects B-D were 90° from the prior transect (Figure 3c). Each transect consisted of pure tones played towards the recorders from logarithmic distances of 10, 20, 40 and 80 m. The tones were generated at 1000 Hz intervals from 1 to 11 kHz from an online signal generator (https://www.wavtones.com/functiongenerator.php), which created five-second sine wave tones at 256 kbit/sec. The speaker was a Harman JBL Charge 3 portable speaker (frequency response 65–20,000, SNR >80 dB). It was always faced towards the recorders and 1.5 m from the ground, after Marten and Marler (1977), as sounds from this height produce the most consistent transmission through forested habitats without suffering loss from ground attenuation. We kept the volume setting constant for all tones, producing signals whose SPLs averaged 80 dB (or ~200,000 microPascals (μPa)) from a one-metre distance. This SPL is the upper limit of an average loud bird call in central European temperate forests (Brumm and Slabbekoorn 2005; Brumm 2009) and is consistent with other studies (Rempel et al. 2013; Darras et al. 2016; Yip et al. 2017b) for comparability.

We programmed both device types to a sampling frequency of 24 kHz, output gain of 25, and to the highest temporal resolution available; the SETs recorded 1 min every other minute and the SM4 recorded continuously. Audio files were saved in Waveform Audio File Format (.wav) on 32 GB SD cards. The five microphones each produced a set of raw .wav files from which we computed our response variables. The SM4 has dual-channel recording (microphones 4 and 5 in Figure 3); thus, it produced one set of wave files for each microphone, which we analysed separately to compare each microphone's response to slope and sound source direction. Temperature and humidity were recorded every other minute by the SETs. These values were averaged per SET per plot per transect.

### 2.4 Data Processing

Transect azimuths were coded according to their relation to plot aspects (aspect always coded as 180°), resulting in a set of directional categories representing the sound source direction (hereafter SSD) in relation to the plot centre: Upslope, Upside (R, right), Side (R), Downside (R), Downslope, Downside (L, left), Side (L), and Upside (L) (Figure 4). The advantage of testing for the potential effect of SSD allowed us to identify the *shape* of each microphone's detection space, not simply the radius of a presumed circle.

We created two response variables to identify the edge of our recorders' detection spaces in eight directions (SSDs) at two spatial scales. The first variable was a binary presence/absence metric from each acoustic test for each frequency. The second variable was calculated using the SPL of the present signals to model the predicted extinction distance for each acoustic test. The extinction distance data are more spatially precise but offer less certainty because they are modelled distances. Conversely, the presence/absence variable was directly observed (more certainty), but at a coarse scale of 10, 20, 40 and 80 m. Our aim in testing both response variables was to identify if the results replicate at two spatial scales, and any differences in model results would aid our interpretation of at which scale the drivers of the detection space were acting.

We converted recordings into spectrograms and manually reviewed them using Wildlife Acoustic Kaleidescope (v.4.0.4). The spectrogram settings were set to optimise visual detection against the background (fft 256, window 128, dB gain 60, dB dynamic range −60). Manual signal detection was computed for recordings from five microphones at each frequency (1–11 kHz) at each distance (10–80 m) on four transects in 16 plots (n = 14,080); we counted strong and weak signals equally as presence, and we counted signals not visible against the background as absence.

To model extinction distance, we first extracted absolute amplitude value (μPa) for each frequency at each distance within a transect. We used the 'spec' function (Seewave package, Sueur et al. 2008) in the R statistical computing environment (R 3.5.2, R Core Team 2018). Each tone was subject to turbulence and therefore presented random fluctuations in SPL; the goal was to identify the maximum possible signal transmission; therefore, we used spectrograms to identify the maximum μPa present in each five-second test (in milliseconds), and directed the spec function to extract SPL from that portion of each sound test.

In order to model the sound extinction distance, it was also necessary to extract ambient μPa values because the detection space is determined partly by the ambient background noise (Ellinger and Hödl 2003; Darras et al. 2016; Turgeon et al. 2017). Ambient noise varies across frequency bands – generally decreasing with frequency – thus we calculated mean ambient SPL for each frequency band in which a test took place. It was not possible to differentiate between extinguished signals (theoretically 0 μPa) and signals whose SPL was simply lower than the ambient noise in that frequency band, so any tones which were undetectable against the background noise were automatically assigned the ambient value at the point in time the signal would have been present. Using tone SPLs at 10, 20, 40 and 80 m, we created logarithmic regressions modelling SPL as a function of distance (see Appendix 1 for details on model choice). From these regressions, we predicted when signal SPL intercepted with the mean ambient SPL extracted from the same test, yielding sound extinction distances for each transect per microphone per frequency (n = 3474). Of the distribution of predictions, the 2.5% and 97.5% quantiles were removed from the dataset (n = 174), as the models at either end of the distribution predicted unlikely or impossible values (Appendix 2). The resulting dataset comprised 3300 predicted sound extinction distances used in subsequent analyses.

## 2.5. Statistical analysis

We conducted all statistical analyses in R version 3.5.2. During initial data exploration, it was evident that there was no effect of humidity, temperature, elevation or any structural variables on either response variable. Thus, the only variables included in the models were categorical fixed effects of frequency (1–11 kHz), microphone orientation (Side (L), Side (R) and Downslope), device (SET or SM4) and SSDs (eight directions).

To test the relative effects of our independent variables, we built generalised linear mixed models (GLMMs) using an information-theoretic approach (Burnham and Anderson 1998) with the 'glmmTMB' package (Magnusson et al. 2017). This approach tests competing *a priori* hypotheses with a set of candidate models, the best model having high predictive value and minimal complexity, with the lowest Akaike information criterion (AIC) value (Akaike 1998). Our study design evaluates multiple interacting variables simultaneously: the potential effect of slope, differences between devices, microphone orientation to the slope, and SSD. Information theoretic modelling is useful for datasets with multiple interacting predictor variables (Garamszegi 2011), measuring the relative strength of evidence for competing hypotheses given the data at hand.

We created two sets of identical candidate models: one using manual signal detection as the response variable (hereafter Detection Models), and the other using the predicted extinction distance as the response variable (hereafter Extinction Models), with a binomial and gamma distribution for each set, respectively. The Extinction Models did not include distance as an independent variable because the response variable itself represents distance. To account for repeated measures per device, all candidate models included device and microphone orientation as fixed effects. All the candidate models hereafter begin with 'M'; candidate models M10 and M15 have alternative model structures for the Extinction Model set, where Device and Mic_orientation were replaced by a composite factor of Microphone_No. (1–5), which contains Mic_orientation and Device in one variable; this was only used in cases where the model would not support both factors. Plot was always included as a random effect. Competing hypotheses affecting signal presence/extinction distance are listed in Table 1, with alternative model structures for M10 and M15 in parentheses.

**Table 1.** Candidate models ranked by lowest AIC value. Top model from both sets of candidate models, Detection Models and Extinction Models are in bold. Included are each model's ΔAIC, rank based on lowest AIC and the Akaike weight (*wi*), which can be interpreted as the approximate probability that a given model performs 'best' in that set of candidate models (Burnham and Anderson 1998). The *wi* describes what percentage of the time, if this experiment were repeated many times, a given model would be the optimal model (lowest AIC).

| | | | Detection Models | | | | Extinction Models | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Hypotheses Tested | Variables constant | rank | ΔAIC | $w_i$ | df | rank | ΔAIC | $w_i$ | df |
| 1 | Frequency | Device + Mic_orientation + (1\|Plot) | 7 | 6587.0 | <0.001 | 15 | 3 | 50.1 | <0.001 | 16 |
| 2 | Distance | Device + Mic_orientation + (1\|Plot) | 4 | 1206.2 | <0.001 | 6 | - | - | - | - |
| 3 | Mic_orientation | Device + (1\|Plot) | 14 | 7155.6 | <0.001 | 5 | 10 | 552.4 | <0.001 | 6 |
| 4 | SSD | Device + Mic_orientation + (1\|Plot) | 12 | 7143.1 | <0.001 | 12 | 7 | 539.7 | <0.001 | 13 |
| 5 | Frequency*Distance | Device + Mic_orientation + (1\|Plot) | **1** | **0** | **1** | **26** | - | - | - | - |
| 6 | Frequency*Mic_orientation | Device + (1\|Plot) | 9 | 6617.8 | <0.001 | 35 | 4 | 68.5 | <0.001 | 36 |
| 7 | Frequency*Device | Mic_orientation + (1\|Plot) | 6 | 6571.3 | <0.001 | 25 | 2 | 26.1 | <0.001 | 26 |
| 8 | Frequency*SSD | Device + Mic_orientation + (1\|Plot)+ (Mic_No + (1\|Plot)) | 10 | 6672.9 | <0.001 | 92 | 5 | 82.1 | <0.001 | 94 |
| 9 | Distance*Mic_orientation | Device + (1\|Plot) | 5 | 1209.0 | <0.001 | 8 | - | - | - | - |
| 10 | Distance*Device | Mic_orientation + (1\|Plot) | 3 | 1205.2 | <0.001 | 7 | - | - | - | - |
| 11 | Distance*SSD | Device + Mic_orientation + (1\|Plot) | 2 | 1163.7 | <0.001 | 20 | - | - | - | - |
| 12 | Mic_orienation*Device (Mic_No) | (1\|Plot) | 15 | 7158.0 | <0.001 | 7 | 9 | 549.5 | <0.001 | 7 |
| 13 | Mic_orientation*SSD | Device + (1\|Plot) | 11 | 7066.1 | <0.001 | 26 | 6 | 521.8 | <0.001 | 27 |
| 14 | Device*SSD | Mic_orientation + (1\|Plot) | 13 | 7147.3 | <0.001 | 19 | 8 | 540.4 | <0.001 | 20 |
| 15 | Mic_orientation*SSD + Frequency | Device + (1\|Plot) | 8 | 6592.2 | <0.001 | 18 | **1** | **0** | **1** | **37** |

## 3. Results

### 3.1. Signal detection and modelled extinction distances

Manual signal detection decreased with increasing frequency and distance. Up to 40 m, 95.5% of the signals were detected across all frequencies and devices, which decreased to 60.7% at 80 m. Across plots, from 1 to 11 kHz, we detected 76.5%, 89.6%, 93.9%, 91.9%, 87.7%, 78.3%, 79.3%, 78.3%, 76.8%, 76.2% and 68.4% of signals, respectively. Exceptions to the pattern were 1 and 2 kHz, which were more often undetectable due to higher ambient noise in those frequency bands. This pattern replicated for modelled extinction distances (Figure 5). We observed the same pattern by device type; both devices' extinction distance and variance decreased with frequency, although the SM4 variance was greater than SETs. The SM4 produced higher manual signal detection rates and predicted extinction distances than the SETs (Chi square = 247.83, $p < 0.001$, df = 1; two-sided Fisher's Test $p < 0.001$, respectively). Ambient noise was also higher for SM4 recordings (Chi square = 2277, $p < 0.001$, df = 1), and for both devices the ambient noise was consistent from all SSDs, except in the 1 kHz band (Appendix 3). Within SETs, we pooled all frequencies and found no difference in predicted extinction distances between microphone orientation (Chi square = 0.27, p = 0.87, df = 2) or SSD (Chi square = 0.85, p = 0.99, df = 7). Repeated for the SM4, we also found no difference in predicted extinction distances between microphone orientation (Chi square = 0.06, p = 0.80, df = 1) or SSD (Chi square = 6.40, p = 0.49, df = 7).

**Table 2.** Parameter estimates for best Detection Model, M5. The variance of the intercepts for random effect plot is 0.7333 (SD ± 0.8563). Significance thresholds denoted by '*' 0.05, '**' 0.01 and '***' 0.001.

| Parameter | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|
| (Intercept) | 4.495053 | 0.320451 | 14.027 | < 2E-16 *** |
| Frequency2000 | 2.563473 | 0.59812 | 4.286 | 1.82E-05 *** |
| Frequency3000 | 3.53619 | 0.875686 | 4.038 | 5.39E-05 *** |
| Frequency4000 | 2.453042 | 0.625653 | 3.921 | 8.83E-05 *** |
| Frequency5000 | 3.027432 | 0.628339 | 4.818 | 1.45E-06 *** |
| Frequency6000 | 0.907838 | 0.360273 | 2.52 | 0.011740 * |
| Frequency7000 | 1.544991 | 0.397243 | 3.889 | 0.000101 *** |
| Frequency8000 | 1.699413 | 0.39982 | 4.25 | 2.13E-05 *** |
| Frequency9000 | 1.417539 | 0.377821 | 3.752 | 0.000176 *** |
| Frequency10000 | 1.887662 | 0.397626 | 4.747 | 2.06E-06 *** |
| Frequency11000 | 1.042662 | 0.352808 | 2.955 | 0.003123 ** |
| Distance | −0.078515 | 0.003874 | −20.269 | < 2E-16 *** |
| Mic_orientationSide (L) | 0.015807 | 0.099191 | 0.159 | 0.873386 |
| Mic_orientationSide (R) | −0.104788 | 0.098883 | −1.06 | 0.289273 |
| DeviceSM4 | 1.78574 | 0.085809 | 20.811 | < 2E-16 *** |
| Frequency2000:Distance | −0.009984 | 0.008289 | −1.205 | 0.228361 |
| Frequency3000:Distance | −0.012061 | 0.011589 | −1.041 | 0.297992 |
| Frequency4000:Distance | −0.002349 | 0.008635 | −0.272 | 0.785634 |
| Frequency5000:Distance | −0.021036 | 0.008627 | −2.438 | 0.014758 * |
| Frequency6000:Distance | −0.011894 | 0.005773 | −2.06 | 0.039365 * |
| Frequency7000:Distance | −0.019853 | 0.006172 | −3.217 | 0.00129 ** |
| Frequency8000:Distance | −0.024927 | 0.006254 | −3.986 | 6.73E-05 *** |
| Frequency9000:Distance | −0.024212 | 0.006075 | −3.985 | 6.74E-05 *** |
| Frequency10000:Distance | −0.033932 | 0.006392 | −5.308 | 1.11E-07 *** |
| Frequency11000:Distance | −0.043525 | 0.006884 | −6.323 | 2.57E-10 *** |

### 3.2. Detection models

M5 best described the observed variation in signal presence/absence data (*wi* = 1, Table 1). M5 parameter estimates (Table 2) reflect results described above, showing that the signal detection probability decreases with increasing frequency and distance. Moreover, the interaction between these two variables affects higher frequencies more strongly: the coefficients increase in significance and negative value as frequency increases. By frequency, the SM4 has significantly higher detection probability than SETs (Figure 6). Microphone orientation was not a significant parameter (Table 2); Figure 7 depicts the same trend for all three microphone orientations. Further, Figure 7 illustrates differences when microphone orientation interacts with SSD, although confidence intervals generally overlap: the detection probability for Side (L), Side (R) and Downslope orientations is highest when they align with SSDs from the same directions.

### 3.3. Extinction models

Similar to the Detection Models set, one model in the Extinction Models set, M15, performed better than any other (*wi* = 1, Table 1). The hypothesis tested by M15 was that in addition to frequency, extinction distance is driven by the interaction between the direction a microphone faces with the direction of the sound source. M15 parameter estimates (Table 3) show that in addition to significant differences between devices and most frequencies, microphone orientation Side (R) and its interaction with SSD Upside (R) significantly, positively affected extinction distance. Other interaction combinations were not significant; however, a positive trend can generally be observed between mean predicted extinction

**Table 3.** Parameter estimates for best Extinction Model, M15. The variance of the intercepts for the random effect plot is 0.009 (SD ± 0.097). Significance thresholds denoted by '*' 0.05, '**' 0.01 and '***' 0.001.

| Parameter | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|
| (Intercept) | 4.48493 | 0.050351 | 89.07 | < 2e-16 *** |
| Mic_orientationSide (L) | −0.026052 | 0.035177 | −0.74 | 0.458935 |
| Mic_orientationSide (R) | −0.09252 | 0.035174 | −2.63 | 0.00853 ** |
| SSDDownside (R) | −0.007613 | 0.039986 | −0.19 | 0.849003 |
| SSDDownslope | 0.101534 | 0.06188 | 1.64 | 0.100834 |
| SSDSide (L) | 0.011338 | 0.062227 | 0.18 | 0.855422 |
| SSDSide (R) | 0.025987 | 0.06202 | 0.42 | 0.675214 |
| SSDUpside (L) | −0.05892 | 0.040495 | −1.45 | 0.145672 |
| SSDUpside (R) | −0.06743 | 0.040599 | −1.66 | 0.096742 |
| SSDUpslope | −0.044125 | 0.062319 | −0.71 | 0.478917 |
| Frequency2000 | 0.135286 | 0.018263 | 7.41 | 1.29e-11 *** |
| Frequency3000 | 0.18378 | 0.018051 | 10.18 | < 2e-16 *** |
| Frequency4000 | 0.151043 | 0.018208 | 8.3 | < 2e-16 *** |
| Frequency5000 | 0.079716 | 0.018321 | 4.35 | 1.36e-05 *** |
| Frequency6000 | −0.010154 | 0.018602 | −0.55 | 0.585169 |
| Frequency7000 | −0.033004 | 0.018797 | −1.76 | 0.079115 |
| Frequency8000 | −0.052043 | 0.018687 | −2.78 | 0.005354 ** |
| Frequency9000 | −0.059458 | 0.01882 | −3.16 | 0.001581 ** |
| Frequency10000 | −0.066422 | 0.018822 | −3.53 | 0.000417 *** |
| Frequency11000 | −0.114326 | 0.019013 | −6.01 | 1.82e-09 *** |
| DeviceSM4 | 0.110942 | 0.008781 | 12.63 | < 2e-16 *** |
| Mic_orientationSide (L):SSDDownside (R) | −0.04039 | 0.049501 | −0.82 | 0.414533 |
| Mic_orientationSide (R):SSDDownside (R) | 0.073645 | 0.049202 | 1.5 | 0.134447 |
| Mic_orientationSide (L):SSDDownslope | −0.058015 | 0.044372 | −1.31 | 0.191059 |
| Mic_orientationSide (R):SSDDownslope | −0.037567 | 0.044554 | −0.84 | 0.39913 |
| Mic_orientationSide (L):SSDSide (L) | 0.082703 | 0.044654 | 1.85 | 0.064015 |
| Mic_orientationSide (R):SSDSide (L) | 0.065753 | 0.044925 | 1.46 | 0.143302 |
| Mic_orientationSide (L):SSDSide (R) | −0.006855 | 0.044595 | −0.15 | 0.877829 |
| Mic_orientationSide (R):SSDSide (R) | 0.086816 | 0.044413 | 1.95 | 0.050611 |
| Mic_orientationSide (L):SSDUpside (L) | 0.072953 | 0.049945 | 1.46 | 0.144102 |
| Mic_orientationSide (R):SSDUpside (L) | 0.06889 | 0.049873 | 1.38 | 0.167187 |
| Mic_orientationSide (L):SSDUpside (R) | 0.068315 | 0.049753 | 1.37 | 0.169722 |
| Mic_orientationSide (R):SSDUpside (R) | 0.183008 | 0.049621 | 3.69 | 0.000226 *** |
| Mic_orientationSide (L):SSDUpslope | 0.045091 | 0.04499 | 1 | 0.316222 |
| Mic_orientationSide (R):SSDUpslope | 0.065199 | 0.045058 | 1.45 | 0.147895 |

distances when microphone orientation and SSD align (Figure 8). SM4 extinction distance variance is greater than the SETs, but SET variance increased when the microphone orientation faced the SSD (Figure 9), further supporting this trend. Although these interactions were often not significant, the M15 hypothesis including this interaction was the best model describing the factors influencing the signal extinction distance.

# 4. Discussion

## *4.1. General patterns*

The factors most strongly affecting signal detection and extinction distance were frequency, distance (for the Detection Models set) and device type, results which were consistent in both best-performing models. Lower frequencies had significantly higher detection probabilities and extinction distances compared to higher frequencies, with the exception of 1–2 kHz. The SM4 device had higher detection probabilities and extinction distances across all frequencies.

Our results are consistent with previous research that detections decline with distance (Venier et al. 2012; Castro et al. 2019) and frequency (Marten and Marler 1977; Price et al. 1988; Rempel et al. 2013; Darras et al. 2016; Yip et al. 2017b). As extinction distance increased, variance per frequency decreased. This too is consistent with previous research (Yip et al. 2017a). Richards and Wiley (1980) found low frequencies were more subject to atmospheric turbulence and higher frequencies experienced a steady decay in acoustic energy. Amplitude fluctuations and reverberations were identified as the primary cause, which differentially affect low and high frequencies, resulting in higher variation in low-frequency signals. Darras et al. (2016) also found that sound waves were more focused and suffered less loss with increasing distance, such that directivity increased with frequency, supporting our observed higher variance in lower frequencies. This effect was stronger with the SM4 than the SET, likely due to higher SNR reported by manufacturers (80 vs. 60 db, respectively) and its ability to detect more of the variations naturally arising in our field tests.

In model visualisations by frequency (Figures 6 and 8), there is a distinct grouping of means into mid (2–5 kHz) and high (6–11 kHz) frequencies. The exception is low frequency (defined in the literature as ≤1 kHz), which degrades similarly to 6 kHz. We attribute this to higher background noise in the lowest frequency band, as well as increased ground attenuation for frequencies ≤1 kHz (Appendix 3). Although signal detection and extinction distance decrease stepwise by frequency, this grouping suggests a pattern that can be generalised into two groups, which may be more useful than individual frequency patterns depending on research or conservation goals. Most acoustic studies report detection spaces ≤100 m, generally assuming that all vocalising species within this radius are equally detected. However, the frequencies between 2 and 5 kHz travel markedly higher distances than the frequencies above and below that range. The implications of this depends on species of interest: anurans typically vocalise between 2 and 5 kHz (Vargas-Salinas and Amézquita 2014); although many cricket species vocalise between 2 and 8 kHz, some species vocalise as high as 30 kHz (Robillard et al. 2013). Low pitched bird species such as owls and pigeons will have a detection space very different from most passerines, which call between 2 and 8 kHz. If a target species generally calls within the high-frequency grouping (6–11 kHz), the detection space could differ by a mean of ~20 m compared to the 2–5 kHz group (Figure 9), violating the 100 m assumption. Likewise, detection probability (P) is higher for species calling in the 2–5 kHz range ($P_{SM4} > 0.70$, $0.25 < P_{SET} < 0.75$) than for higher-calling species in the 6–11 kHz range ($P_{SM4} < 0.75$, $P_{SET} < 0.25$) at our 80 m test.

### 4.2. SSD and microphone orientation

Microphone orientation in relation to slope was rarely a significant parameter across all models and there is little evidence to suggest an overall effect of microphone orientation on detection space on sloped terrain. In the one instance when the parameter was significant, so was the interaction with SSD in the same direction (model M15, Table 3); overall patterns suggest that this significant effect of microphone orientation was due to the microphone's interaction with SSD, not due to its relation to slope, an effect which would occur on flat terrain as well as slopes.

Despite their advertised omnidirectionality, microphones of both high and low-cost classes have a bias towards the direction they face. Although the trend is consistent across both models (Figures 7–8), this effect was often not statistically significant, likely due to high variation in the data and the relatively small effect size of this interaction compared to the major drivers of signal transmission (frequency, distance and device). This bias was not a driver of presence/absence data, as evidence by M5 and not M15 as the best-performing model in the Detection set. This suggests that this interaction matters at the finer spatial scale (extinction set) because it affects signal transmission at distances of 5–10 m (Figures 8 and 9) and could not be detected between 40 and 80 m presence/absence tests (detection set). Microphone orientation in relation to slope therefore does not affect extinction distance, but rather its relation to SSD does.

Interestingly, this SSD interaction affects the low-cost microphones (SETs) differently. While both devices produce slightly higher mean extinction distances when microphone orientation and SSD align, the variance of the SET data is what primarily responded to the interaction: SET variance increases only when microphone orientation and SSD aligns, whereas the SM4 variance is consistent throughout all SSD combinations (Figure 9). This change in variance, not mean values, partially explains why these trends do not produce more consistently significant results. Furthermore, we have thus far discussed each SM4 microphone individually, while in reality the combination of these two channels would be used in acoustic analyses. When one combines the directionality of microphones 4 and 5, the detection space is subject to even less SSD bias. Together this indicates that SM4 microphones via stereophonic recording are more omnidirectional than SETs, for which the bias is stronger for the lower quality microphone with monophonic recording capabilities.

Despite their name, omnidirectional microphones are not truly omnidirectional; they have a loss of sensitivity towards the back of the microphone, which is compounded by the sound shadows cast from the typically box-shaped device they protrude from and the tree trunk upon which the devices are usually installed. The polar response of a microphone allows us to determine how omnidirectional it truly is, which varies based on its shape, size, and mounting to the body of the device. Polar responses are often not made readily accessible by the manufacturers (as is the case for both of our devices); however, in more traditional (non-biology) recording industries, it is common practice to include the microphone's polar response. Furthermore, polar responses are frequency dependent (Earthworks Audio 2020), whereby lower frequencies are subject to less directional bias. We observed this effect in our results as well: the directionality of both recorders increased with frequency. This has implications for accurate sampling methodology; some microphones should be used preferentially given the vocalising frequencies of the species of research interest, and the distribution of recorders throughout a recording area should be adjusted based on the polar response of microphones on a given ARU. To aid in reducing misunderstandings about the detection space of ARUs, we recommend manufacturers publish the frequency-dependent polar response of their microphones, particularly when advertising with the 'omnidirectional' descriptive term. Darras et al. (2018) recommends at least two omnidirectional microphones facing opposite directions to cover a greater, more consistent sampling space, and our results support this recommendation, given that both of the SM4 microphones combined produce a more consistent detection space. Hence, we support Darras et al.'s recommendation as a solution to bypass inconsistencies in polar response and omnidirectionality.

Finally, the SET downslope orientation tended to have a slightly larger relative detection space (Figure 8), particularly for 2–5 kHz sounds originating downslope from the microphone. These findings support Hunter (1989), who found 77% of observed bird vocalisations faced uphill. This provides slight evidence that vocalising downslope from the intended receiver (i.e., recording from above the sound source) may be optimal for signal transmission. However, this orientation produces a difference of ~5 m, with overlapping confidence intervals (Appendix 5). Although these biases were rarely statistically significant due to high variability in our data, the pattern was consistently observed, and we therefore recommend to account for whenever resources allow. We recommend keeping the number of microphones and orientation consistent across all study sites to maintain a consistent detection space *shape*. Given that a downward microphone orientation seems to produce a slightly more pronounced bias compared to either side orientation, when recording with dual-channel recorders, we recommend that they are installed perpendicular to the slope, such that one side does not have a more pronounced bias than the other. When recording with single-channel recorders and resources do not allow for two facing opposite directions, we likewise recommend a perpendicular orientation, given that its detection space is, if anything, slightly more circular (Figure 8).

The microphone orientation – SSD interaction effect is small and the variability in our data is high, so we could not identify strong significant differences, underscoring the general difficulty in precisely defining detection spaces. This is consistent with findings by Castro et al. (2019) that generally, high variability exists between ARUs, with no singular predictor explaining the variation. Despite standardising the weather conditions and forest structure in our experimental setup, both the SET and SM4 had high standard deviation around mean extinction distances (89.5 ± 23.8 m and 100.9 ± 29.5, respectively). Acoustic signals are subject to constant flux and as such, a range of probable detection distances under certain standardised conditions is the best approximate description we can achieve for any device.

### 4.3. Differences between devices

The SM4 produced significantly greater detection probability and extinction distances than SETs. These results are in slight conflict with Rempel et al. (2013), who tested six recorder types (price range: US$250-$7000) and found no difference in birdsong detection between recorder type. However, most species call within a range of frequency bands; thus, our analysis comparing devices by individual frequencies was more fine-scaled, which may explain why we found significant interactions and Rempel et al. did not. Additionally, they tested different devices with SNRs different than that of our devices, and SNR is well established as a critical driver of detection distances (Darras et al. 2020).

Advantages of device choice extend beyond cost and microphone specifications (i.e., SNR, microphone sensitivity and quality). These include ease of programmability, flexibility of recording schedules, battery life, data storage capacity and format, durability, weight, size and if they come ready to use or require housing to be built by the consumer.

Frequency response and target distance are additional factors that researchers must weigh (see Appendix 6 for full discussion on frequency response); for research conducted on slopes, our results suggest higher-quality microphones, especially with stereo recording capabilities, more successfully detect signals at greater distances, particularly in the high-frequency range, with less directional bias (Figure 8). However, this difference is only on average a difference of 11.4 m across frequencies, past 50 m. If researchers attempt to make recordings with the largest detection space possible, the SM4 performs better. However, if the primary interest in acoustic recordings is to capture vocalisations loud enough to identify species, or for vocalisations to register on soundscape index computations >50 dB thresholds; then, SM4s and SETs perform similarly well because louder calls typically occur under 50 m, and both devices capture strong signals at those distances. It should be noted that our SETs were prototypes, and presumably the commercially available device would have performed as well or better, however even the prototype (lower-quality microphone) performed similarly to the SM4 (higher-quality microphone) under 50 m (Figure 6).

### *4.4. Plot-level metrics*

None of our plot metrics were included in the candidate models. Generally, sound propagation studies agree that differences between sites within a habitat classification are unimportant (Aylor 1972; Wiley and Richards 1978; Lambert and McDonald 2014). Moreover, Darras et al. (2016) found that vegetation structure measures such as DBH, tree density, BA, understory vegetation density and height were poor predictors of sound transmission within a habitat. While the effects of scattering, refraction and absorption by vegetation contribute to sound attenuation at a very fine scale, the consensus is their effect size is not strong enough to matter between sites within the same habitat (Marten and Marler 1977), which our results confirm. All recorders, regardless of price or quality, experience a high degree of fluctuation in detection space, and these effects are too small to be captured within such large variation. Plot-level metrics, like the microphone orientation – SSD bias, matter at a fine spatial scale, but for the purposes of acoustic recording at ~100 m radius within the same habitat type, they do not.

### *4.5. Experimental versus natural recording conditions*

In several ways, our estimates were conservative. First, manual signal detection revealed weak but visible signals at 80 m tests on spectrograms, ranging from 20 to 200 μPa, which we still counted as presence. Our predicted extinction distances too were conservative because we modelled signal SPL equal to ambient SPL; however, it is likely that in a natural setting the signal would need to be several decibels above ambient sound in order to be aurally detected. For example, Darras et al. (2016) set a 4 dB threshold above ambient values for identifying bird calls from recordings.

Second, after spectrogram settings were adjusted to maximally identify faint signals, the SPL from the strongest part of the tone was always extracted such that any detection differences found between devices or orientations represented the least difference between detection capabilities. This too is a conservative approach given that the strongest part of the signal can last a short duration and therefore be insufficient for realworld surveys, such as identifying species by song (bioacoustics), or transmitting enough data to drive differences in acoustic indices (ecoacoustics), which often use default 50 dB thresholds. However, it was the most standardised approach, and any significant differences found between microphone orientations would be equal to or slightly greater in actuality, rather than weaker.

Wind also affects detection radius by affecting transmission distance and increasing ambient noise. Yip et al. (2017b) found that when they experimentally manipulated white noise conditions to mimic low and high winds typical in the area, the effective detection radius was reduced 25–44% for loud species and an average of 93% for quiet-calling species. In high-wind scenarios, wind would be a much larger driver of detection space than microphone orientation in relation to slope; therefore, we recommend orient microphones out of the prevailing wind direction (Müller et al. 2020), which minimises recording unwanted geophony to better capture targeted biophony. Likewise, we recommend adjustments if the microphone is located inside weatherproof housing, in which case length and shape of the detection space changes more dramatically (Shaw and Müller (2020), unpublished data) and adjustments should be made according to pre-test results for that particular device-housing combination.

Next, our speakers were always directed towards the microphones, but birds do not always face the microphone, thus shortening the distance from which their vocalisations would be heard. For birds calling below 80 dB, the distances from which microphones could capture their vocalisations are further shortened. Lastly, directivity will also vary; the directivity of our speaker was standardised for all tests, but directivity of bird calls vary per species, per call per species. Yorzinski and Patricelli (2010), for example, observed antipredator calls were broader than calls to conspecifics, which were more narrowly focused. Our study quality would be improved if we also tested different shapes of bird calls such as burst and sweeps to test if different sound envelopes also influence the detection space. Taken together, our calculations represent maximal transmission distances in quiet, little-to-no wind scenarios with optimised sound source directionality, pure tones and standardised directivity. Greater variation and shorter overall transmission distances would likely be found in natural recording conditions.

## 5. Conclusions

Our results provide the first evidence documenting patterns of microphone orientation in relation to slopes and its implications for recorder detection space. The primary effects observed in this study will hold true on flat terrain, namely the attenuation of sound with increasing distance and frequency, and differences between high- and low-cost devices. Our findings suggest microphone orientation in relation to slope is not an important methodological consideration, and more dominant factors such as frequency, distance and prevailing wind direction drive detection space shape. The shape of detection space is not precisely circular, as microphones are biased in the direction they face, but higher-quality microphones, stereo recording and a perpendicular orientation to slope tend to provide a more omnidirectional detection space. With a growing use of acoustic recorders in biodiversity research, so increases the need to standardise recording protocol for better comparability between studies. Although the factors affecting sound transmission are complex, our aim in describing them is to identify an installation procedure that captures the widest range of frequencies at the most uniform radius, thereby more precisely implementing the advantages of acoustic monitoring as a conservation science tool.

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## Ethical statement

Our study followed the institutional and national ethical guidelines for scientific research in Germany.

## Authors' contributions

TS and SM conceived the ideas and designed methodology; TS collected and analysed the data and led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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## Data availability statement

The data that support the findings of this study are available from the corresponding author, [TS], upon reasonable request.

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