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Of walls and floors: how physical structures affect mating song detection in stridulating orthopterans

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Abstract

1. Sensory ecology theory proposes that modalities like vision, audition and olfaction determine habitat selection and behavioural adaptation by organisms. This study explores how physical modifications in the environment influence the probability of detecting mating songs of stridulating orthopterans (suborder Ensifera) in nature. By experimentally introducing floors and walls into vegetated fields, we demonstrated that such structural changes can either enhance or hinder sound propagation and song detection, depending on species-specific acoustic traits.
2. Song detection probability increased for Nemobiinae species, likely due to improved sound reflection or behavioural attraction to the structures. Conversely, detection of Conocephalinae species decreased in the presence of these structures, suggesting adverse effects on habitat quality and signal transmission. Phaneropterinae species showed no clear response, likely owing to their long-range song propagation from elevated positions. Song detection was also influenced by air temperature, time of day, vegetation density and microphone position, with warmer temperatures and elevated microphone positions generally enhancing detection.
3. Structural changes to vegetated fields altered not only sound propagation but also potentially species incidence and behaviour. These findings highlight the interplay between the modification of physical structures and species traits. Our results underscore the need for habitat-specific conservation strategies, particularly in settings where both acoustic and physical environments are continually transformed, such as in urbanised areas.

KEYWORDS
ecoacoustics, Ensifera, singing insects, song propagation, sound attenuation

INTRODUCTION

The theory of sensory ecology conceptualises the environment as a mosaic of signals (e.g., physical structures, sounds, odours) interacting with the sensory traits of organisms (Dominoni et al., 2020; Römer, 1998). It proposes that resource selection and behavioural adaptations are determined by senses such as vision, audition and olfaction. Organisms exhibit a range of sensory traits, which allow them to produce and detect signals of interest against the background environment (Stevens, 2013). In insects, for instance, sensory abilities are modulated by traits such as the eye diameter for vision (Feller et al., 2021; Land, 1997) and the number and types of antennae sensilla for olfaction (Elgar et al., 2018; Nakano et al., 2022). In terms of acoustic communication, it is important to distinguish between signal traits, such as the carrier frequencies produced by sound-producing organs and sensory traits, such as the sensitivity of hearing organs (Meyer & Elsner, 1996; Song et al., 2020), which together determine how sounds are produced, transmitted and detected.

Only a handful of studies in terrestrial ecosystems have experimentally manipulated the acoustic environment to evaluate its impact on animal communities *in situ*. A sound-removal experiment in the United States compared silent natural gas well-pads with noisy compressor stations. This research has shown that noise negatively affected bird fitness (Kleist et al., 2018) and reduced bat species abundance (Bunkley et al., 2015). Another influential experiment broadcasted road traffic sounds at a stopover site during autumn avian migration. The findings revealed that many species, although not all, displayed avoidance behaviour (McClure et al., 2013) and that birds exposed to traffic sounds gained less weight during their stopover (Ware et al., 2015). However, the above studies did not explicitly evaluate how changes to physical structures per se affected the acoustic environment and ultimately animal communities. In practice, changes to one set of environmental features (e.g., physical structures) are often confounded by changes to another set. For example, human activities alter the acoustic environment directly, by affecting sound production and propagation and indirectly by modifying physical structures and species distribution patterns (Proulx et al., 2019).

Stridulating orthopterans of the suborder Ensifera, which includes crickets and katydids, are model organisms for studying the effect of environmental changes (e.g., Rebrina et al., 2022; Schmidt & Balakrishnan, 2015). In the field, they typically reach abundances ranging from 2 to 20 individuals per 10 m^2 depending on the species and type of vegetation (Fartmann et al., 2024). Each species has a unique combination of signal traits that affect how well their songs propagate in the environment. For instance, songs at higher acoustic frequencies tend to travel over shorter distances compared to lower-frequency ones, independently of the power level at the source (Römer, 1998). Additionally, stridulating from the ground increases interference by the litter and surrounding vegetation, further limiting song propagation (Arak & Eiriksson, 1992). Hence, species stridulating at low frequencies and from an elevated position should be considered long-range propagators in comparison to species stridulating from the ground at high frequencies (Römer, 1998).

Physical structures also determine how sounds propagate in the environment. Depending on their size and density, structures made of wood or other materials can cause sound absorption, reflection, or diffraction (e.g., Greenfield, 2002). Stems and leaves also interfere with sound waves by scattering them and degrading the signal (Arak & Eiriksson, 1992; Bennet-Clark, 1998). Other factors, such as air temperature and time of day, will affect both the stridulation activity of Ensifera species and the propagation of sounds (Römer, 1998). For instance, it was shown that the metabolic rate of orthopterans increases linearly with temperature in the range between 15°C and 30°C (Lachenicht et al., 2010), which is likely to influence stridulation activity. Moreover, air temperatures during daytime are lower at the top of the vegetation, causing sound waves to propagate upward and be lost to the atmosphere. After sunset, however, when temperature inversion occurs (i.e., temperatures are lower near the ground), the sounds get trapped and propagate more effectively late in the evening (Sanborn, 2006).

The present study aimed to: (i) identify endogenous traits that can influence song propagation among Ensifera species from four subfamilies present in the St-Lawrence lowlands of Québec, Canada, (ii) establish experimental settings with modifiable physical structures that alter sound attenuation and (iii) evaluate the response of stridulating orthopterans (suborder Ensifera) to modifications of physical structures and acoustic properties. More specifically, we evaluated the probability that a microphone acting as a receiver organism could detect the song of an emitter (e.g., male katydid) in different types of constructed settings. For this purpose, we designed a Before-After-Control-Impact experiment in five vegetated fields (two grasslands, two wet meadows and one fallow field) where we constructed floor and wall structures. We predicted that the song detection of Ensifera taxa in different experimental settings is a function of their stridulating position in the vegetation and song frequencies. On one hand, species living close to the ground and stridulating at high frequencies (short-range acoustic species) should be advantaged by physical structures that enhance sound propagation by increasing ground reflection and decreasing vegetation density. On the other hand, species living at an elevated position in the vegetation and stridulating at low frequencies (long-range acoustic species) should be disadvantaged by structures that increase sound attenuation, since they rely on both their singing position and peak frequencies to propagate their signal.

METHODS

Song propagation traits of Ensifera species

We compiled two traits associated with song propagation in Ensifera species of the Nemobiinae, Oecanthinae, Phaneropterinae and Conocephalinae subfamilies. We studied 14 species that are commonly observed in the region where we conducted the experiments (southern Québec, Canada). Since both stridulating position of the insect within the vegetation and peak frequency are known to influence sound propagation (Arak & Eiriksson, 1992; Römer, 1998), we included these two traits for each species (Table 1). We extracted peak song frequency from audio recordings of Ensifera species published in the Guide sonore et visuel des insectes chanteurs du Québec et de l'est de l'Amérique du Nord (Pelletier, 1995). Each recording has low levels of background interference and lasts between 10 and 30 s. We obtained the peak frequency of each species' song using the *Seewave* R package (Sueur et al., 2008), with the functions 'meanspec' and 'fpeaks' (Hanning window length of 512 with 50% overlap). It corresponds to the frequency value at which the local maximum (peak) of highest amplitude is detected. For each species, we also determined its typical stridulating position in the vegetation (ground, middle, or top) from two sources: The Orthoptera of Michigan (Bland, 2003) and The Insects and Arachnids of Canada, part 14 (Vickery et al., 1985).

TABLE 1 Acoustic traits of 14 orthopteran species in the suborder Ensifera from southeastern Québec, Canada.

Species	Subfamily	Peak frequency (kHz)	Position in the vegetation
Allonemobius allardi; Alexander & Thomas 1959 (Allard's ground cricket)	Nemobiinae	7	Ground
Allonemobius fasciatus; De Geer 1773 (Striped ground cricket)	Nemobiinae	8.5	Ground
Eunemobius carolinus; Scudder 1877 (Carolina ground cricket)	Nemobiinae	5	Ground
Neonemobius palustris; Blatchey 1900 (Sphagnum ground cricket)	Nemobiinae	8.5	Ground
Oecanthus nigricornis; Walker 1869 (Black-horned tree cricket)	Oecanthinae	4.5	Middle
Oecanthus quadripunctatus; Beutenmüller 1894 (Four-spotted tree cricket)	Oecanthinae	3.5	Middle
Oecanthus fultoni; Walker 1962 (Snowy tree cricket)	Oecanthinae	2	Middle
Amblycorypha oblongifolia; De Geer 1773 (Oblong-winged katydid)	Phaneropterinae	9	Top
Scudderia pistillata; Brunner von Wattenwyl 1878 (Broad-winged bush katydid)	Phaneropterinae	11	Top
Scudderia curvicauda; De Geer 1773 (Curve-tailed bush katydid)	Phaneropterinae	10	Top
Scudderia furcata; Brunner von Wattenwyl 1878 (Fork-tailed bush katydid)	Phaneropterinae	9	Top
Neoconocephalus ensiger; Harris 1841 (Sword-bearing conehead)	Conocephalinae	10	Middle
Conocephalus fasciatus; De Geer 1773 (Slender meadow katydid)	Conocephalinae	8	Middle
Conocephalus brevipennis; Scudder 1862 (Short-winged meadow katydid)	Conocephalinae	7.5	Middle

Note: Traits are the peak frequency of the mating song estimated from the power spectrum and the typical position occupied in the vegetation while stridulating.

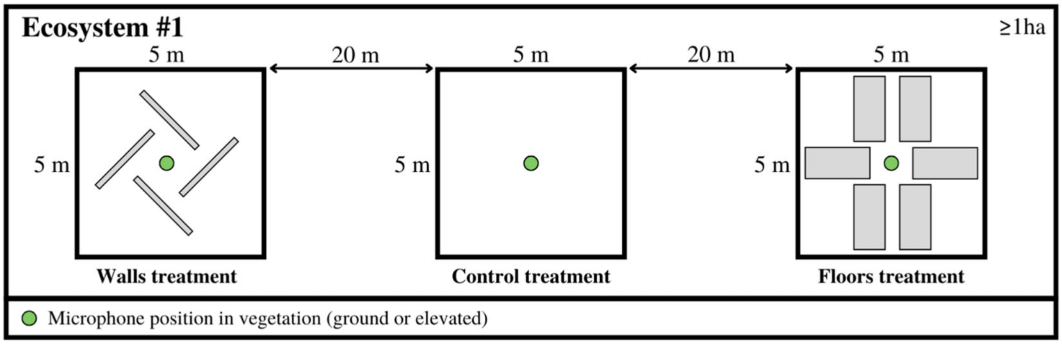

FIGURE 1 Schematic representation of the experimental settings for one field type. Each setting was assigned one of the three treatments (i.e., walls, floors, or control). Each treatment contained an AudioMoth™ (circle), either positioned close to the ground (5 cm) or elevated (60 cm), acting as a receiver organism.

Experimental settings

We modified sound attenuation properties by constructing three experimental settings with modifiable structures: (i) vertical structures (i.e., walls), (ii) no structure (i.e., control) and (iii) horizontal structures (i.e., floors). Each setting consisted of a 5 m × 5 m surface located about 20 m away from the other two settings within the same area (Figure 1). The physical structures had to reflect sounds, be weather-resistant, sturdy enough to withstand wind and have a thermal inertia comparable to the surrounding vegetation. For the present purpose, we selected plywood panels of 13 mm thickness and 0.42 g/cm^3 density. The walls treatment consisted of four panels of size 0.9 m by 1.2 m (total of 4.32 m^2) arranged as a maze, which were held vertically and raised 6 cm above the ground using wooden stakes. The floor treatment consisted of six panels of size 0.6 m × 1.2 m (total of 4.32 m^2), laid horizontally and raised 6 cm above the ground. The control treatment had no panels (Figure 1). We positioned the floor panels by bending the vegetation without removing it.

We conducted acoustic tests on July 24th, 2023, to compare the properties of the three experimental settings in a lawn field at the Université du Québec à Trois-Rivières (46,34,953° N, 72,58,058° W) (Figure 1). We positioned two AudioMoth™ autonomous recorder (Open Acoustic Devices designs, United Kingdom) in each experimental setting, one close to the ground (5 cm height) and the other elevated above the ground (60 cm height on a tripod). A pre-recorded orthopteran chorus was played-back through a speaker (Wonderboom™, Ultimate Ears, Irvine, USA). The playback, obtained from a 1-h recording made on a calm August evening in 2011, featured a natural chorus that included the fall field cricket

TABLE 2 Description of the five vegetated fields where experiments were conducted. All fields were part of a larger protected area on the shore of the St-Lawrence River (Québec, Canada).

Field number	Field type	Vegetation height (cm)	Lat.	Long.	Dominant plant species
1	Grassland	110–125	46.1744683	−73.0326006	*Phalaris arundinacea*, *Vicia cracca*, *Equisetum arvense*
2	Wet meadow	65–75	46.1645181	−73.0714235	*Butomus umbellatus*, *Xanthium strumarium*, *Lythrum salicaria*
3	Fallow field	50–65	46.1616449	−73.0793565	*Asclepias syriaca*, *Eupatorium maculatum*, *Vicia cracca*, *Convolvulus sepium*
4	Grassland	100	46.1654549	−73.0641859	*Phalaris arundinacea*, *Vicia cracca*, *Asclepias incarnata*, *Convolvulus sepium*
5	Wet meadow	100–130	46.1543790	−73.0793203	*Scirpus cyperinus*, *Asclepias incarnata*, *Phalaris arundinacea*, *Typha latifolia*

Note: Each experimental field was characterised based on its typology (grassland, wet meadow, fallow field), vegetation height and composition of dominant plant species.

(*Gryllus pennsylvanicus*) stridulating at peak frequencies around 4.5 kHz, the Allard's ground cricket (*Allonemobius allardi*) stridulating around 6.5 kHz and their harmonics. We positioned the speaker close to the ground (5 cm height) at 5 m away from the microphone. We obtained a 1-min recording of the playback for each microphone in each experimental setting, for a total of six 16-bit WAV audio clips at a sampling rate of 48 kHz. We processed the audio clips using the 'meanspec' function in the *Seewave* R package (Sueur et al., 2008) and visually compared the amplitude spectrum of the various settings. We converted the spectrum values to decibels by setting the reference amplitude to the maximum (parameter dB = 'max0').

Field experiments

To evaluate the response of stridulating orthopterans to our experimental settings, we selected five vegetated fields, each covering at least 1 hectare of uniform plant cover. Each field featured distinct dominant plants and vegetation typologies (Table 2). In all 15 experimental settings (3 treatments × 5 fields), we measured vegetation density using a 1.5 m Robel pole. We delineated the 'walls,' 'floors' and 'control' settings in each of the five fields on July 28th.

We implemented a Before-After-Control-Impact design during the mating season of stridulating orthopterans. We installed the plywood panels on August 13th, 2023. We recorded stridulating orthopterans over two periods: before (August 1st to August 10th) and after (August 16th to September 10th) the deployment of physical structures. Whenever recording, we positioned one AudioMoth™ at the center of each experimental setting, pointing upward to minimise the effect of directional hearing. We recorded sounds simultaneously across all treatment levels and fields from 7 PM to 1 AM and programmed the microphones to record 3 min every 30 min for a total of 12 recordings per evening and setting. From one evening to the next, we alternated the position of the microphone between the ground and elevated from the ground. Each microphone was placed in a protective case and configured to record at a sampling rate of 48 kHz in 16-bit WAV format, with the gain set to the minimum. We deployed microphones as frequently as possible under optimal weather conditions, on warm evenings (≥15°C) and in the absence of rain or strong winds (≤ 10 km/h). In total, we sampled six evenings in the 'before' period and 15 in the 'after' period, producing a total of 3485 audio clips over the season. To obtain a single value of air temperature at each date, we noted the minimum and maximum temperatures registered at the closest weather station over the recording period and calculated the mid-point value as follows: $\frac{\text{min}+\text{max}}{2}$.

Audio clips and statistical analyses

We visualized all audio clips of the field experiments using the spectrogram function in Audacity 3.3.3 (Audacity Team, 2023). We listened to each 3-min clip and inspected the spectrogram to identify all stridulating insects present. Taxonomic identification was confirmed using reference spectrograms from the websites Song of Insects (https://songsofinsects.com) and Singing Insects of North America (https://orthsoc.org/sina). For each clip, we noted the presence or absence of each species or subfamily, which we used as a measure of the instantaneous probability that a mating song was detectable by a human listener at the microphone's position. To ensure consistency, all clips were analysed by the first author using headsets in a calm indoor environment and double-checked a second time by the same person. Singing individuals that could not be confidently identified at the species level were referred to as 'sp'. and assigned to a subfamily. This situation happened when it was difficult to differentiate between two species of the same subfamily.

We inspected the rank incidence distribution of all species and subfamilies by summing presences across audio clips in each of the two periods independently (i.e., before and after). Species and subfamily incidences were represented as absolute frequencies, dividing the sum of presences of a particular taxon in each period by the total number of audio clips.

We tested the response of stridulating orthopterans to the experimental settings in the before and after periods using generalised linear mixed-effects models on the presence–absence matrix. We aggregated presence data at the taxonomic level of subfamilies (i.e., presence–absence of a subfamily) to avoid arbitrarily discarding too many clips containing unidentified species. We fitted one model to each subfamily to evaluate song detection probability using a binomial distribution with a logit link function in the 'glmer' function from the *lme4* package (Bates et al., 2015). More specifically, we tested for an interaction between the treatment variable (three levels; walls, floors and control) and the period (two levels; before and after). We also included the following covariables as fixed effects: recording time of day (from 7 PM TO 1 AM), vegetation density (between 50 and 125 cm), air temperature (from 14 to 26°C), microphone position (two levels; ground and elevated) and the field typology (five levels). We included the recording date (21 evenings) and the AudioMoth™ identifier (15 devices) as random effects in our models. For comparison purposes, we fitted the same model structure only to the most common species in each subfamily. We did not make a technical distinction between detection and occupancy probabilities, which becomes irrelevant when the number of repeat surveys is high as in our case (McNeil & Grozinger, 2020).

We used the 'predictorEffects' function in the *effects* package (Fox & Weisberg, 2018) to evaluate how the song detection probability of each subfamily, defined here as the likelihood that a mating song is detected by a human listener in an audio clip, changes according to the covariables and experimental design variables. The probability is estimated at the predictor values by fixing the other variables at their respective means. Standard errors are estimated using the sample covariance matrix of the model coefficients. Four predictor values were selected for the following covariables: recording time of day (6 PM, 8 PM, 10 PM, 12 AM), vegetation density (Robel height; 60 cm, 80 cm, 100 cm, 120 cm), air temperature (15°C, 18°C, 21°C, 25°C) and microphone position (ground, elevated). The design variables consisted of the three levels of the experimental treatment (walls, floors, control), two periods (before, after) and their interaction.

RESULTS

Song propagation traits of Ensifera species

We observed that traits related to song propagation discriminated Ensifera species at the taxonomic level of subfamilies (Table 1). Nemobiinae species in our pool stridulate from the ground with peak frequencies between 5 and 8.5 kHz, whereas Conocephalinae species stridulate from an intermediate position with peak frequencies ranging between 7.5 and 10 kHz. In comparison, Phaneropterinae species stridulate from the top of the vegetation at peak frequencies between 9 and 11 kHz, whereas Oecanthinae species stridulate from mid-vegetation between 2 and 4.5 kHz. Therefore, the songs of Nemobiinae and Conocephalinae are expected to propagate over shorter distances due to either excess attenuation by the vegetation (Nemobiinae) or high-frequency signalling (Conocephalinae). In contrast, the songs of Phaneropterinae and Oecanthinae are expected to propagate over longer distances due to either weak interference by the vegetation (Phaneropterinae) or low-frequency signalling (Oecanthinae). All else being equal, the mating songs of Nemobiinae and Conocephalinae species are predicted to propagate over shorter distances than the songs of Oecanthinae and Phaneropterinae.

Experimental settings

Preliminary tests revealed changes to acoustic properties after the structures were introduced to the environment (Figure 2). Compared to the control treatment, the microphone recorded higher sound levels in the presence of floors and lower levels in the presence of walls. The microphone's position also influenced the amplitude spectrum, with higher sound levels captured by the elevated microphone compared to the one near the ground (Figure 2). The largest differences in sound levels between treatments occurred around 4.5 kHz and 13 kHz, which correspond to the dominant frequencies and harmonics of the species stridulating in the playback. The average difference between elevated and ground microphones in the control was 5.1 dB across the whole spectrum (1–20 kHz). Considering only the elevated microphone at dominant frequencies (from 4 to 5 kHz and from 12.5 to 13.5 kHz), the average difference between walls and control settings was −2.5 dB, while the average difference between floors and control settings was +4.9 dB (Figure 2). Walls attenuated Ensifera songs, whereas floors propagated them.

Field experiments

Species composition

We observed the presence of all Nemobiinae, Conocephalinae and Phaneropterinae species among the two periods (Figure 3). The most frequently detected species was the Carolina ground cricket (*E. carolinus*), with an absolute incidence of 65% before the modifications and 99% after the deployment of structures (Figure 3). We excluded this species from subsequent analyses because it was present in nearly all audio clips and offered no discriminatory power. We also excluded species from the Oecanthinae subfamily, this time because of very low incidence rates (<1% in the before period and 5% in the after period).

Effect of covariables on song detection probability

We tested the effect of covariables on the song detection probability of subfamilies, irrespective of treatment or period. The first effect we considered was the time of day at which the recording was made (Figure 4). For two subfamilies, the Nemobiinae and the Conocephalinae, the probability decreased as the time of day went on (Nemobiinae: $z = -9.129$, $p < 0.001$; Conocephalinae: $z = -20.450$, $p < 0.001$). However, we observed the opposite trend for individuals

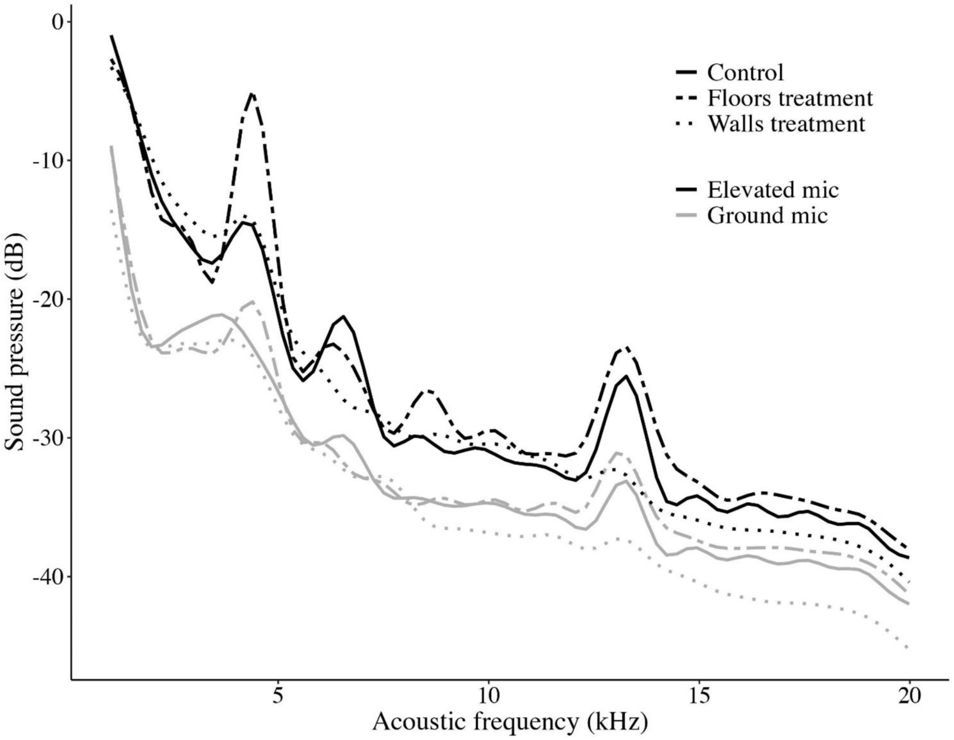

FIGURE 2 Smoothed power spectra of the playback sounds recorded in three experimental settings over a lawn field: No structure (Control treatment; solid line), horizontal plywood panels (Floors treatment; dashed line) and vertical plywood panels (Walls treatment; dotted line). Each line represents the power spectrum of stridulating orthopterans from a pre-recorded chorus replayed through a speaker. Playback sounds were recorded by two AudioMoth™ microphones; one at the top (Elevated mic; black lines) of the vegetation and the other at the bottom (Ground mic; grey lines).

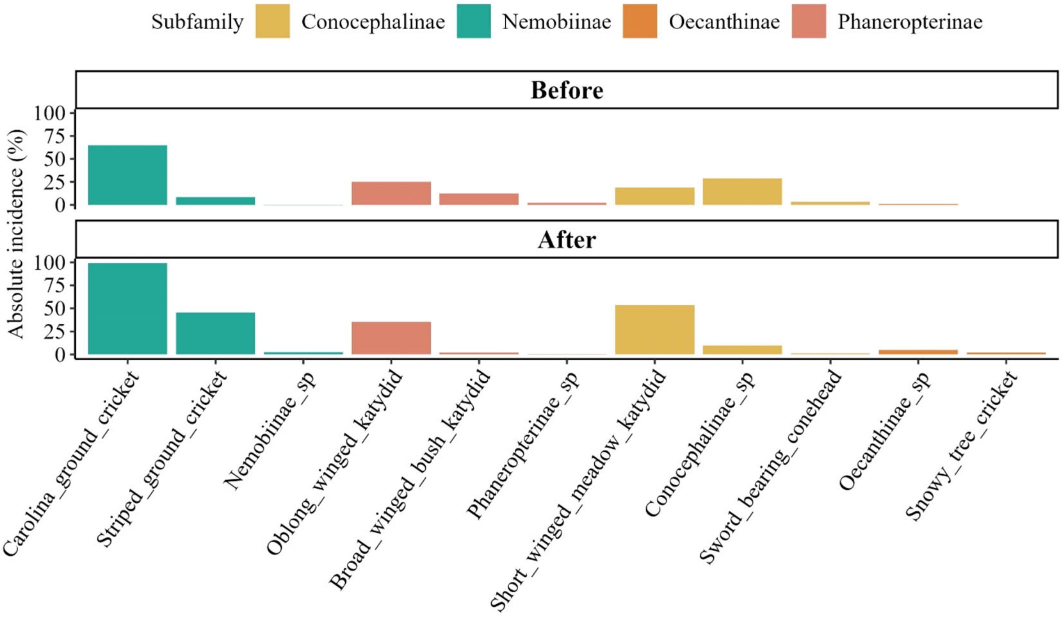

FIGURE 3 Absolute incidence (%) of each taxon during the two periods of the field experiment; before and after the installation of physical structures. The before period contained recordings made between August 1 and August 10, 2023, while the after period was recorded between August 16 and September 10, 2023. Each bar represents the absolute detection incidence of a species across every audio clip obtained in each period, with species coloured according to their respective subfamily (colour legend).

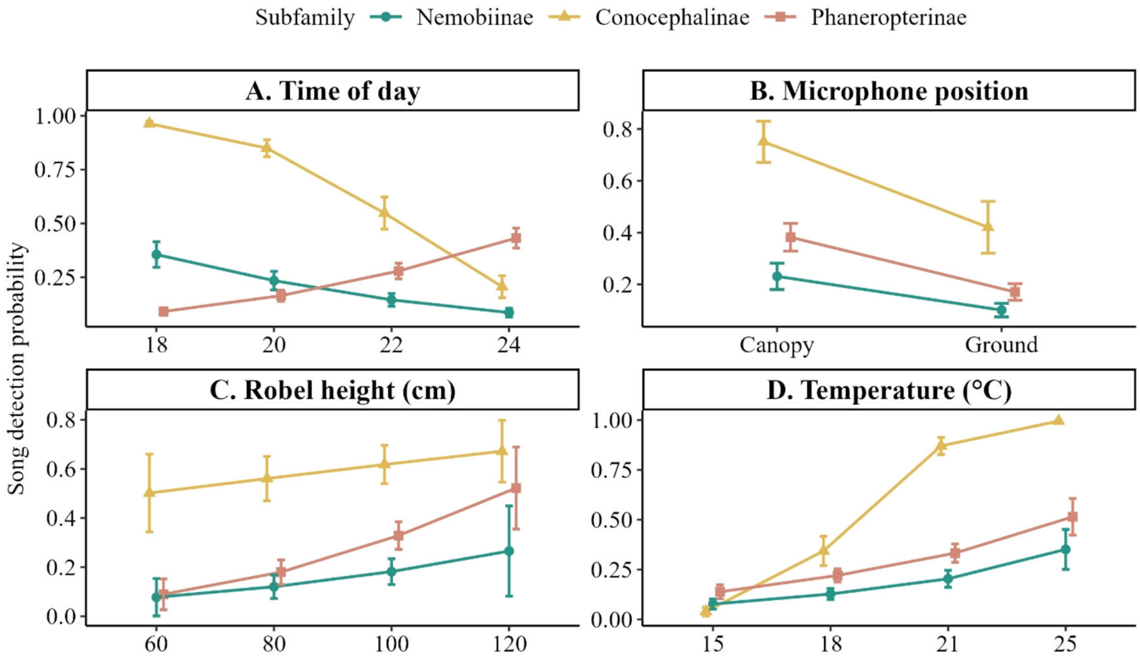

FIGURE 4 Effect of the time of day (a), the microphone position (b), the Robel height (c) and the air temperature (d) on the song detection probability of the three subfamilies studied during the field experiment. The four covariables analysed here are the recorded time of day (6 PM, 8 PM, 10 PM and 12 AM), the microphone position (ground or elevated), the Robel height representing the vegetation density (cm) and the mid-point temperature of each night recorded (°C). Each subfamily is represented by a different symbol and colour: Nemobiinae (green circle), Conocephalinae (yellow triangle) and Phaneropterinae (red square). Means and standard errors were obtained by setting the other model predictors at their respective means.

of the Phaneropterinae, since their probabilities increased through the evening ($z = 12.388$, $p < 0.001$).

We also considered the effect of microphone position on the song detection probability of the three subfamilies (Figure 4b). As expected, the probability was lower when the microphone was elevated from the ground for Nemobiinae ($z = -3.062$, $p = 0.002$), as well as for the Conocephalinae ($z = -2.450$, $p = 0.014$) and the Phaneropterinae ($z = -4.054$, $p < 0.001$).

The third effect considered was Robel height, which is a measure of vegetation height and density (Figure 4c). All three subfamilies showed a flat to slightly positive relationship between vegetation height and song detection probability. However, the relationship was not statistically significant (Nemobiinae: $z = 0.750$, $p = 0.453$; Conocephalinae: $z = 0.679$, $p = 0.497$; Phaneropterinae: $z = 1.728$, $p = 0.084$).

For all subfamilies, the song detection probability increased with increasing air temperature (Nemobiinae: $z = 2.923$, $p = 0.003$; Conocephalinae: $z = 6.990$, $p < 0.001$; Phaneropterinae: $z = 3.416$, $p < 0.001$). This effect was particularly strong for the Conocephalinae, ranging from a probability close to zero at 15°C to nearly one at 25°C (Figure 4d).

Finally, we tested the effect of field identity on the song detection probability of subfamilies (Suppl. Mat.). The results revealed sharp differences among fields for all subfamilies. The Nemobiinae and Phaneropterinae were predominant in the fallow field site but had low detection probabilities in the grassland sites, whereas wet meadows returned intermediate probabilities. In contrast, Conocephalinae songs were predominant in grassland sites but had lower detection probabilities in the fallow field and wet meadows (Supp. Mat.).

Effect of physical structures on song detection probability

The main objective of the experiments was to test for the effect of physical structures on the song detection probability of stridulating orthopterans in nature. Our results reveal that detection probability increased for individuals of the Nemobiinae subfamily when structures were present (Figure 5a). The probability nearly doubled on average between the control and the structure treatments (Figure 5a). However, these trends were not always supported by the model's statistics (floors treatment: $z = 2.454$, $p = 0.014$; walls treatment: $z = 0.237$, $p = 0.812$).

We observed the opposite response for individuals of the Conocephalinae subfamily, which were detected less often in the presence of structures, especially walls (Figure 5b). Even though the song detection probability changed moderately, on average, between treatment levels, the model's statistics strongly supported an interaction between period and treatment (floors: $z = -2.649$, $p = 0.008$; walls: $z = -2.927$, $p = 0.003$).

The probability of detecting individuals of the Phaneropterinae subfamily was highest in the walls treatment and lowest in the floors

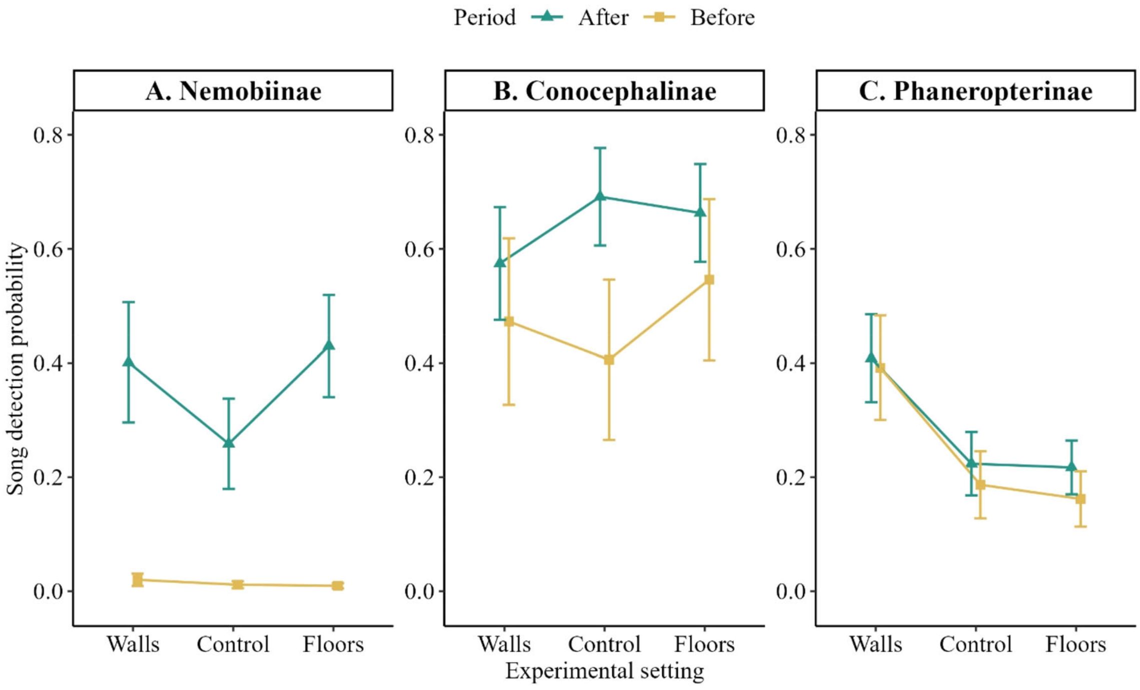

FIGURE 5 Effect of experimental settings (Walls, Control and Floors) on the song detection probability of the Nemobiinae (a), the Conocephalinae (b) and the Phaneropterinae (c). The two periods are before any modifications and after the deployment of physical structures. Means and standard errors were obtained by setting the other model predictors at their respective means.

treatment, both before and after the deployment of structures (Figure 5c). There was no interaction between treatment and period for the walls ($z = -0.668$, $p = 0.504$), nor for the floors ($z = 0.538$, $p = 0.591$), suggesting that the structures had little influence on the song detection probability of Phaneropterinae.

We performed additional analyses to evaluate our models using only the most common species of each subfamily. The effect sizes and directions at the species level are consistent with those reported at the subfamily level, although the model's statistics sometimes differ (Supp. Mat.). The level of taxonomic aggregation did not change the interpretation of results, although the patterns were emphasised at the subfamily level.

DISCUSSION

We found that modifying the physical structures, and thus acoustic properties, of the experimental settings affected the detection probability of mating songs of orthopteran species. We showed that the deployment of floor and wall structures respectively increased and decreased song propagation in open fields. The song detection probability of individuals of the Nemobiinae subfamily increased in both wall and floor settings relative to the control period (i.e., no structures). We observed the opposite pattern for individuals of the Conocephalinae subfamily, for which the probability decreased when structures were present. The two other subfamilies investigated in this paper either did not respond to the presence of physical structures in our BACI design (Phaneropterinae) or were not detected often enough to warrant a full assessment (Oecanthinae). Nevertheless, the detection probability of mating songs was strongly modulated by the receiver position, time of day, air temperature and vegetation typology for all subfamilies.

Song propagation traits of Ensifera species

We predicted that species living close to the ground and stridulating at high frequencies should be advantaged by physical structures increasing song propagation, whereas species living at an elevated position in the vegetation and stridulating at low frequencies should be disadvantaged by structures increasing sound attenuation. We compiled the signal traits of 14 Ensifera species and identified two main groups. The 'short-range species' propagate their songs over shorter distances. This group includes individuals of the Nemobiinae subfamily, which stridulate from the ground, leading to rapid sound attenuation by the litter and surrounding vegetation, and individuals of the Conocephalinae subfamily, which stridulate at high frequencies, causing sounds to travel over shorter distances. In contrast, the 'long-range species' propagate their songs over longer distances. This group includes individuals of the Phaneropterinae subfamily, which stridulate from elevated positions, and of the Oecanthinae subfamily, which stridulate at low frequencies. More generally, the functional role of the above traits is encapsulated by the 'Mass law' (Ebbitt & Hansen, 2007), which states that excess attenuation is proportional to sound frequencies (kHz) multiplied by the density of physical structures (kg m^{-3}) in the signals' travel path.

Detection of stridulating orthopterans in nature will be affected by signal traits, by sound attenuation in the signals' travel path, but also by the activity and incidence of adults. An example in our experiment is the Carolina ground cricket, which had an absolute incidence of 99% in the 'After' period; the species was very active and detected in nearly all audio clips. It is important to recognise that the addition of floor and wall structures did not only impact song propagation and sound attenuation but perhaps also the incidence of species and subfamilies within the experimental settings, potentially due to habitat partitioning. Specifically, the artificial floor placed directly on the ground likely provided shelter and suitable microhabitats for ground-dwelling crickets (Nemobiinae), which commonly seek refuge under rocks and dense objects (Bland, 2003). This habitat modification may have contributed to the increased incidence of these species. In contrast, the walls treatment is expected to have fewer direct effects on vegetation structures and thus less influence on the incidence of this species.

Covariables' effect on song detection probability

Based on our results, air temperature and time of day modulated the stridulation activity of orthopterans in all subfamilies, and therefore their probability of song detection. We observed that the probability of detecting mating songs increased with increasing air temperature. To our knowledge, this is one of the first assessments of the temperature response of these taxa in nature. The rate of increase was also steeper for the Conocephalinae than for the other two subfamilies. In general, our results on the probability of song detection support the linear response between temperature and metabolic activity previously reported in laboratory experiments for two *Gryllus* species (Jang & Gerhardt, 2007) and for the house cricket (*Acheta domesticus*) (Lachenicht et al., 2010).

While some environmental variation between dates of recording was captured by air temperature throughout the mating season, time of day captured the variation within a particular evening. We expected the song detection probability at the microphone's position to decrease through the evening, since the cooling of air temperature after sunset should also reduce stridulating activities (Sanborn, 2006). This is precisely the pattern we observed for the Conocephalinae and Nemobiinae subfamilies. However, individuals of the Phaneropterinae showed the opposite response, as the probability increased with time of day. We identified two possible explanations. First, species of this subfamily engage in acoustic duets, when both male and female are stridulating concomitantly (Heller et al., 2015). The likelihood of finding a mate using this behaviour might increase by avoiding acoustic interference with other species. Second, species of the Phaneropterinae produce songs that propagate over long distances due to their elevated position in the vegetation, even though they stridulate at relatively high frequencies. Hence, the temperature inversion that occurs late in the evening, which traps sounds between the ground and the warmer air above, might act as a waveguide that compensates for the high frequencies of their mating songs (Römer, 1998; Sanborn, 2006).

Our results showed that the probability of song detection increases when the microphone is positioned away from the ground for all subfamilies, which aligns with the prediction that vegetation acts as a barrier to song propagation (Arak & Eiriksson, 1992). Yet, we also found that the vegetation height of the experimental settings did not have a strong influence on the detection probability. However, the effect of vegetation density and height was partly confounded with the effect of field identity in our experimental design. Another possibility is that dense vegetation stands host a higher incidence of stridulating orthopterans by offering food and nesting resources, as well as protection against predators (e.g., Robinson & Hall, 2002). In such cases, the effect of sound attenuation on detection probability in high and dense vegetation stands could be counterbalanced by a higher incidence for some species.

Treatment effect on song detection probability

We predicted that subfamilies with short-range song propagation should be advantaged by structures increasing sound reflection, while the long-range species should be disadvantaged by the same structures, especially walls. Our predictions were only partially supported by the experiment. In the following section, we interpret our results for each subfamily in light of song propagation, sound attenuation and vegetation properties.

Nemobiinae

Results for the Nemobiinae subfamily showed that the probability of detection increased in the presence of plywood structures. The introduction of floor and wall structures did not appear to directly alter the habitat of cricket species living within the litter. In fact, we frequently observed during fieldwork many Nemobiinae individuals crawling on the floor structures. It is possible that they actively selected these reflective structures to increase the propagation of their songs, and therefore their detection. However, we cannot rule out that the plywood structures also accumulated more heat inertia and, therefore, were selected more intensively for stridulating. Thus, it is unclear if the observed pattern only highlighted a change in singing behaviour, or also in incidence (i.e., attraction effect). While future experiments are needed to disentangle these mechanisms, the main result that physical structures increased the detection of mating songs holds for this subfamily, although it might not be solely related to changes in acoustic properties.

Conocephalinae

Contrary to our predictions, both floor and wall structures negatively affected the probability of detecting songs of the Conocephalinae subfamily. These insects rely on their elevated position in the vegetation to avoid predators, access food and increase song propagation (Capinera et al., 2004; Römer, 1998). Hence, the floor structures placed on the existing vegetation did impact their preferential habitat. Such habitat alteration could translate into a reduction of incidence, and therefore a lower probability of detection in the presence of floors. In contrast, we observed during fieldwork that Conocephalinae individuals actively selected wall structures, which is in line with their behaviour of perching in the middle of the vegetation. Since microphones only recorded one side of the walls, individuals perched on the other side may have gone undetected, leading to a lower probability of song detection. Previous studies on Conocephalinae species found that they are negatively associated with constructed habitats (McNeil & Grozinger, 2020) and strongly depend on a cover of high vegetation (Kenyeres et al., 2024). Our findings support the interpretation that the deployment of physical structures negatively affects the song detection of Conocephalinae.

Phaneropterinae

In support of our prediction, the experiment revealed that floor structures had no effect on the probability of detecting songs of Phaneropterinae. However, song detection probability also did not change before and after the introduction of wall structures, which is contrary to our prediction. These results suggest that Phaneropterinae were not affected by habitat degradation or acoustic changes caused by the floor and wall structures at this spatial scale. Individuals of this subfamily are known to produce songs that travel over long distances by perching at the top of the vegetation (Capinera et al., 2004). Since the wall structures in our experiment were about 1 m high, it is possible that they did not interfere with their mating songs. Indeed, three out of our five ecosystems had vegetation reaching above the walls, as measured by the Robel height. We also observed plant stems reaching above this threshold in the field. Alternatively, it is possible that the stridulating individuals of this subfamily were too far outside the experimental settings and, therefore, not affected by the structures. For example, a study conducted in Germany reported much lower densities for the Phaneropterinae species in comparison to the Conocephalinae species (Fartmann et al., 2024).

The present study is one of the first attempts to manipulate the physical structures and the acoustic properties of vegetated fields. As such, we identified some limitations that could be addressed in future studies. Firstly, disentangling the compounded responses of insects to changes in physical structures, acoustic properties, or other sensory modalities remains challenging. Some of our results and field observations suggest that the physical structures may have been selected irrespective of their acoustic properties. Secondly, the probability of detecting a mating song using microphones depends on two key assumptions: (i) the recording abilities of the device and (ii) the accurate detection of songs through spectrogram analyses. Our ability to identify a song does not necessarily mean that the signal quality is preserved or that it effectively communicates important information to potential mates, such as male's fitness. Furthermore, signal detection by a human observer, based on spectrogram analyses, does not equate to the recognition by conspecifics. Insects possess highly specialised auditory systems, including frequency tuning, directional hearing and neural filtering, which shape how they perceive and localise sounds. Therefore, while our approach estimates signal detectability, it does not capture the full complexity of an effective communication in singing insects.

CONCLUSION

Understanding the influence of land-use changes on sound-dependent animals has become an increasingly prominent issue. Nevertheless, few studies have thoroughly examined how these modifications impact various taxonomic groups or effectively differentiated between the physical and acoustic alterations involved. This study investigated the responses of three subfamilies of singing insects within the suborder Ensifera to changes in physical structures and acoustic properties, revealing distinct patterns in each subfamily. Findings indicate that the Nemobiinae subfamily shows an adaptive capacity to these changes, while the Conocephalinae subfamily's limited response appears to be primarily driven by specific habitat requirements rather than acoustic constraints. In contrast, the Phaneropterinae subfamily remained largely unaffected by both acoustic and physical alterations in the environment. This is one of the first experiments that manipulate the environment's physical properties to unravel how signal traits possibly modulate the response of organisms to environmental changes. Our results underscore the need for habitat-specific conservation strategies, particularly in urban areas where both acoustic and physical environments are continually transformed.

AUTHOR CONTRIBUTIONS

Laurie Provençal: Investigation; writing – original draft; methodology; visualization; conceptualization; data curation. **Raphaël Proulx:** Conceptualization; funding acquisition; writing – original draft; methodology; visualization; writing – review and editing; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. This research did not require any specific ethical permits.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from the Borealis Digital Repository (Provençal & Proulx, 2025): https://doi.org/10.5683/SP3/SMKT52.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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