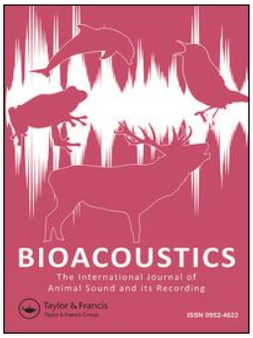


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# Sound production in bark and ambrosia beetles

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**ABSTRACT**

Bark and ambrosia beetles and pinhole borers (Coleoptera: Curculionidae: Scolytinae and Platypodinae) are two subfamilies of weevils that use acoustic communication within plant tissue. These insects transmit and detect sound in a medium that is neither air nor water and they are among the smallest animals with sound-producing organs. Nevertheless, their sound production is sorely understudied, mostly due to the difficulties associated with acoustically monitoring individuals inside plants. We analysed the stridulatory sounds from 55 bark and ambrosia beetle species within 15 subtribes collected in four countries, making this the largest acoustic dataset of these taxa to date. We characterised and compared the amplitude and spectro-temporal parameters of the distress airborne signals produced by the beetles, in conjunction with phenology and life history data. Sound production was present in 33% of the collected species, of which 60% of these sounds had not been previously reported. Depending on species, either both sexes stridulated or only one. Some species had calls with different acoustic morphotypes (one, two, or three notes), and when both sexes stridulated, sounds generally differed. Our data suggest that type of mating system and size play an important role in determining the acoustic communicatory capacity of most species.

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## Introduction

The range of distances over which organisms communicate, in conjunction with the medium they inhabit, dictates what communication mode is possible or most effective (Bossert and Wilson 1963; Naguib and Wiley 2001). Acoustic signals allow for communication in substrates where visual and chemical modes are not reliable (Römer 1998; Hill 2008). For example, organisms that live and breed in chemically-saturated habitats, such as tide pools, or in the dark, such as caves or trees, often rely on sound as a mode of communication (Proakis et al. 2001; Gerhardt and Huber 2002).

Bark beetles and pinhole borers (Coleoptera: Curculionidae, Scolytinae and Platypodinae) are among the many insects that reside and communicate within plant

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tissue (Vega and Hofstetter 2015), which, unlike water or air, is a medium seldom addressed in communication studies (Hill et al. 2019). These beetles are known as bark and ambrosia beetles, where the term ambrosia refers to a common feeding mode (xylomycetophagy, or mutualistic fungus farming) that evolved independently multiple times within both subfamilies (Kirkendall 1983; Hofstetter et al. 2015). Bark and ambrosia beetles tend to construct tunnels and oviposit within trees (bark beetles typically in phloem; ambrosia beetles in xylem) where adults and larvae feed and complete their development (Vega and Hofstetter 2015). This is a common, but not universal, characteristic of bark and ambrosia beetles, as pith-feeding (myelophagy) and fruit and seed-feeding (spermatophagy) also occur in a variety of taxa (Kirkendall 1983). In some ambrosia beetle species, colonies may persist for several years within the tree, with overlapping generations and life stages within a family unit (i.e. a tunnel system) (Kirkendall 1983). Aggressive tree-killing bark beetles typically have only one generation within a tree, with little or no overlap between life stages (Six and Bracewell 2015), and secondary bark beetles may use the host tree for several generations, depending on moisture and phloem decay rates. Some bark and ambrosia beetles use pheromones to synchronise attacks on trees, or simply to attract mates over long distances, but may use acoustic signals over short distances (particularly within the tree or at the tree surface) (Rudinsky 1969; Rudinsky and Michael 1972; Birch 1984). The beetle that initially colonises the tree and releases pheromones may be male or female, depending on species (Vega and Hofstetter 2015). In Scolytinae, stridulatory structures are often sexually dimorphic and less-developed or absent in the sex that initiates tunnel construction, regardless of where on the body the stridulatory organ is located (Barr 1969; Hofstetter et al. 2019). This is a common feature in the family Curculionidae where the stridulatory organ often plays an important role in sexual selection (Lyal and King 1996). Nonetheless, stridulatory structures can also be used in other behavioural contexts, including pair formation, rivalry, distress, copulation, pheromone production, and species recognition (Bedoya et al. 2019a; Barr 1969; Ryker and Rudinsky 1976; Lyal and King 1996).

Despite the purported importance of acoustic signals in bark beetles (e.g. Rudinsky 1969; Rudinsky and Michael 1972; Ryker 1984), the signals of only a handful of bark and ambrosia beetle species have been investigated thoroughly. Acoustic signalling appears to be widespread in bark beetles (Barr 1969; Lyal and King 1996), although less so in ambrosia beetles (Ohya and Kinuura 2001; Kirkendall et al. 2015). The Scolytinae and Platypodinae used to be categorised as closely-related subfamilies due to their morphological and behavioural similitudes (Wood and Bright 1992). However, recent phylogenetic studies support a separate origin for both subfamilies (Gillett et al. 2014; Mugu et al. 2018). Acoustic communication is present in at least half of the subtribes of the Scolytinae (Barr 1969; Lyal and King 1996), and it is a common trait among the rest of the CCCMS clade of the Curcolionidae (Conoderinae, Cossoninae, Curculioninae, Molytinae, Scolytinae) (Lyal and King 1996). However, sound production is not ubiquitous and is absent in either one or both sexes in several species. In contrast, sound production is the rule among the Platypodinae and is often found in both sexes (Menier 1976; Ytsma 1988; Lyal and King 1996).

The power of the emitted stridulatory signals of these beetles indicates that these are close range signals and potentially detectable by conspecifics within a few centimetres of

the signaller within the tree (Fleming et al. 2013). Although nothing is known about the possible acoustic receptors in bark and ambrosia beetles (Hofstetter et al. 2019), sound production has evolved several times (Barr 1969; Lyal and King 1996). Three primary stridulatory mechanisms within bark beetles (Scolytinae) are known: elytro-tergal, vertex-pronotal, and gula-prosternal stridulatory organs (Barr 1969). In pinhole borers (Platypodinae), only the elytro-tergal stridulatory mechanism is known to occur (Ytsma 1988; Lyal and King 1996). Bark and ambrosia beetles produce a variety of call types that vary in temporal characteristics and frequency ranges. General call types appear relatively consistent within genera (Rudinsky and Michael 1974; Yturralde 2013), although intraspecific differences occur between chirps produced in different contexts (Bedoya et al. 2019a; Rudinsky and Michael 1972; Fleming et al. 2013).

Here, our overarching aim is to appreciably add to the information on bark and ambrosia beetle acoustics to begin to understand the evolution of their acoustic communication. The specific objectives of this study are to (*i*) characterise the temporal, spectral, and amplitude features of airborne sounds produced by bark and ambrosia beetles across multiple tribes and genera, and (*ii*) compare the characteristics of the distress/disturbance signals produced across beetle species.

## Materials and methods

### *Collection of experimental specimens*

A total of 55 bark and ambrosia beetle species were assessed for signal production. Specimens (Table 1) were collected in the United States (Arizona, California, Florida, Georgia, Michigan, Texas), New Zealand (Canterbury, Auckland, Westland), Spain (Canary Islands), and Colombia (Antioquia). This dataset contains phloeophagus (wood-feeding), xylomycetophagus (ambrosia-feeding), and spermatophagous (seed-feeding) species across 15 subtribes of Scolytinae and Platypodinae, including most of New Zealand's platypodines. All sound-producing species were recorded using the same equipment at two facilities (University of Canterbury, NZ; Northern Arizona University, USA).

### *Experimental setup and acoustic data collection*

Sounds were recorded inside a purpose-built soundproof box (w × l × d, 250 × 300 × 100 mm). Individuals were adhered with reusable putty-like adhesive (Blu Tack™) from the antero-dorsal part of the elytra in an upside-down position on top of an acrylic surface. This allowed all the specimens to be recorded at a fixed distance from the microphone without restricting any of the movements needed for sound production, thus standardizing signal acquisition. The elytra are the static part of the compound stridulatory organ in beetles with elytro-tergal stridulation (Lyal and King 1996). In the other two stridulatory mechanisms, i.e. gula-prosternal and vertex-pronotal, it does not play any active role. Distress signals were elicited by physically touching the beetle on the abdomen with a soft paintbrush (Bockingford, 5700R, size 1) and were recorded using an ultrasonic microphone (3 Hz to 50 kHz frequency range and flat frequency response; M50, Earthworks Inc., Milford, NH) positioned 20 mm from the individual's stridulatory organ. Signals were recorded with a four channel SD 744T audio

**Table 1.** List of the collected bark and ambrosia beetle species. **Sample** (number and sex of tested/recorded individuals, ♂: male, ♀: female, **n**: not identified), **Sound** (species that stridulated, **Y**: yes, **N**: no), **Sex** (gender with sound production capabilities), **Organ** (type of stridulatory organ, **E-T**: elytro-tergal, **V-P**: vertex-pronotal, **G-P**: gula-prosternal), **Location** (where the specimens were collected). See supplementary material 2 for the authority of the species named.

| Tribe: Subtribe | Beetle species | Sample | Sound | Sex | Organ | Location |
|---|---|---|---|---|---|---|
| Hylesinini: Hylastina | *Hylastes ater* | 10 ♂ 20 ♀ | Y | ♂ | E-T | Canterbury, NZ |
| Hylesinini: Hylastina | *Hylastes porculus* | 1 ♀ | N | | | Georgia, USA |
| Hylesinini: Hylastina | *Hylurgops subcostulatus* | 1 ♂ | Y | ♂ | E-T | Arizona, USA |
| Hylesinini: Hylesinina | *Hylesinus aculeatus* | 12 ♂ 15 ♀ | Y | ♂ | E-T | Texas, USA |
| Hylesinini: Hylurgina | *Hylurgus ligniperda* | 10 ♂ 30 ♀ | Y | ♂ | E-T | Canterbury, NZ |
| Hylesinini: Phloeosinina | *Phloeosinus dentatus* | 8n | N | | | Texas, USA |
| Hylesinini: Phloeosinina | *Phloeosinus cupressi* | 12 ♂ 12 ♀ | Y | ♂ | E-T | Canterbury, NZ |
| Hylesinini: Phloeotribina | *Phloeotribus liminaris* | 2n | N | | | Texas, USA |
| Hylesinini: Polygraphina | *Carphoborous bicornis* | 1 ♂ 2 ♀ | N | | | Georgia, USA |
| Hylesinini: Tomicina | *Dendroctonus brevicomis* | 4 ♂ 2 ♀ | Y | ♂ ♀ | E-T* | Arizona, USA |
| Hylesinini: Tomicina | *Dendroctonus frontalis* | 8 ♂ 13 ♀ | Y | ♂ ♀ | E-T* | Arizona, USA |
| Hylesinini: Tomicina | *Dendroctonus terebrans* | 1 ♂ | Y | ♂ | E-T | Georgia, USA |
| Hylesinini: Tomicina | *Dendroctonus adjunctus* | 4 ♂ 6 ♀ | Y | ♂ | E-T | Arizona, USA |
| Hylesinini: Tomicina | *Dendroctonus pseudotsugae* | 7 ♂ 8 ♀ | Y | ♂ | E-T | Arizona, USA |
| Hylesinini: Tomicina | *Pachycotes peregrinus* | 30n | N | | | Westland, NZ |
| Platypodini: Platypodina | *Platypus apicalis* | 10 ♂ 2 ♀ | Y | ♂ ♀ | E-T | Westland, NZ |
| Platypodini: Platypodina | *Platypus gracilis* | 2 ♂ 2 ♀ | Y | ♂ ♀ | E-T | Westland, NZ |
| Platypodini: Platypodina | *Treptoplatypus caviceps* | 5 ♂ 13 ♀ | Y | ♂ | E-T | Canterbury, NZ |
| Platypodini: Platypodina | *Euplatypus parallelus* | 2 ♂ 1 ♀ | Y | ♂ ♀ | E-T | Florida, USA |
| Scolytini: Corthylina | *Gnathotrichus deleoni* | 6n | N | | | Georgia, USA |
| Scolytini: Corthylina | *Gnathotrichus sulcatus* | 4n | N | | | Georgia, USA |
| Scolytini: Corthylina | *Gnathotrichus materiarius* | 2n | N | | | Florida, USA |
| Scolytini: Corthylina | *Monarthrum mali* | 3n | N | | | Florida, USA |
| Scolytini: Corthylina | *Monarthrum fasciatum* | 9n | N | | | Florida, USA |
| Scolytini: Corthylina | *Pityophthorus consimilis* | 3n | N | | | Florida, Georgia, USA |
| Scolytini: Corthylina | *Pityophthorus concentralis* | 1n | N | | | Florida, USA |
| Scolytini: Corthylina | *Pityophthorus confusus* | 11 ♂ 1 ♀ 9n | N | | | Georgia, USA |
| Scolytini: Corthylina | *Pityophthorus annectens* | 2 ♂ 1n | N | | | Georgia, USA |
| Scolytini: Corthylina | *Pityophthorus pulicarius* | 1 ♂ | N | | | Georgia, USA |
| Scolytini: Corthylina | *Pityophthorus juglandis* | 2n | N | | | California, USA |
| Scolytini: Corthylina | *Pityophthorus liquidambarus* | 1 ♀ | N | | | Georgia, USA |
| Scolytini: Corthylina | *Pseudopityophthorus minutissimus* | 1 ♀ | N | | | Texas, USA |
| Scolytini: Cryphalina | *Hypothenemus hampei* | 5 ♂ 8 ♀ | N | | | Antioquia, Colombia |
| Scolytini: Cryphalina | *Hypothenemus eruditus* | 1 ♀ | N | | | Georgia, USA |
| Scolytini: Cryphalina | *Hypocryphalus sp.*** | 25n | N | | | Canterbury, NZ |
| Scolytini: Dryocoetina | *Dactylotrypes longicollis* | 10 ♂ 10 ♀ | N | | | Canary Islands, Spain |
| Scolytini: Ipina | *Ips pini* | 10 ♂ 24 ♀ | Y | ♀ | V-P | Arizona, USA |
| Scolytini: Ipina | *Ips avulsus* | 24 ♂ 10 ♀ | Y | ♀ | V-P | Georgia, USA |
| Scolytini: Ipina | *Ips grandicollis* | 30 ♂ 19 ♀ | Y | ♀ | V-P | Georgia, USA |
| Scolytini: Ipina | *Ips calligraphus* | 10 ♂ 13 ♀ | Y | ♀ | V-P | Arizona, USA |
| Scolytini: Ipina | *Ips confusus* | 8n | N | | | Arizona, USA |
| Scolytini: Ipina | *Orthotomicus latidens*† | 13n | N | | | Arizona, USA |
| Scolytini: Ipina | *Orthotomicus caelatus* | 1n | N | | | Florida, USA |
| Scolytini: Scolytina | *Scolytus multistriatus* | 11 ♂ 7 ♀ | N | | | Auckland, NZ |
| Scolytini: Scolytina | *Scolytus ventralis* | 6 ♂ 3 ♀ | Y | ♂ ♀ | G-P | Arizona, USA |
| Scolytini: Scolytina | *Scolytus rugulosus* | 30n | N | | | Michigan, USA |
| Scolytini: Xyleborina | *Ambrosiodmus obliquus* | 1 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Xyleborus gracilis*†† | 1 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Xylosandrus crassiusculus* | 30 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Xylosandrus germanus* | 1 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Xyleborus glabratus* | 2 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Xyleborus affinis* | 1 ♀ | N | | | Florida, USA |
| Scolytini: Xyleborina | *Xyleborinus saxesenii* | 5 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Cnestus mutilatus* | 8 ♀ | N | | | Georgia, USA |
| Scolytini: Xyleborina | *Dryoxylon onoharaense* | 9 ♀ | N | | | Florida, Georgia, USA |

†*synonym with Ips latidens;* ††*synonym with Xyleborinus gracilis; *Elytro-tergal in males, Sterno-tergal in females (*Rudinsky and Michael 1973*); **undescribed New Zealand endemic species; particularly small (mean ± sd, 1.70 ± 0.07 mm) and colonises lemonwood and wineberry.*

recorder (Sound Devices LLC, Reedsburg, WI, USA) at a sampling frequency of 96 kHz, 48 dB gain, and 24 PCM bit depth.

### Analyses

Recordings were automatically segmented using a threshold based-approach on the mean power distribution in the temporal domain (Bedoya et al. 2019a, 2019b). Every call was then independently-analysed in order to extract seven spectro-temporal features. An IIR high pass filter, order 4, at 100 Hz was used to remove the DC offset. Four spectral (maximum, minimum, centroid, and dominant frequencies) and three temporal features (call duration, inter-call interval, and call rate) were selected to describe and compare the recorded species (see Bedoya et al. 2019a for expanded definitions and descriptions). Spectrograms for the computation of the spectro-temporal features were obtained using a flat top-weighted window of size 1024 samples and 768 sample overlap. The size of the FFT was 1024 samples. All reported features were based on the mean values of the spectro-temporal parameters of the individuals within each species (see Table 1 for sample sizes). The discrete-time pressure signal (incident to the microphone) was related to the normalised recording samples by $p_i[n] = (V_{ref}/S{\cdot}G)\ x[n] = 1.2114x[n]$. where $S = 36{\cdot}10^{-3}$ is the microphone sensitivity, $G = 10^{48/20} = 251.189$ (48 dB) is the recorder gain, and $V_{ref} = 10.0545$ is the recorder full-scale voltage. Sound Pressure Level (SPL) spectrums and spectrograms were computed using $L_p[n] = 20\log10(p_i[n]/p_0)$, where $L_p$ is the SPL signal, and $p_0 = 20$ μPa is the reference sound pressure in air. A Principal Component Analysis (PCA) was used to reduce the dimensionality of the data and to compare the acoustic differences among the studied species. Before analysis, all the spectro-temporal features were normalised (0–1) to reduce scale effects. The PCA was estimated using single value decomposition, and the principal components were ordered by the magnitude of their singular values. The automatic call detection, parameter estimation, and PCA were performed in Matlab 2018b. The general description and comparison of the bark beetle sounds was based on the terminology described in Bedoya et al. (2019a).

## Results

Our dataset consisted of species from the three bark and ambrosia beetle tribes: Hylesinini, Scolytini, and Platypodini, and contains recordings of the three main types of stridulatory organs (Figure 1). Most species differed in their use of host material, feeding mode, and mating system. This is the first time the stridulatory structures are imaged for the species exemplified in Figure 1 (i.e. *Euplatypus parallelus, Ips avulsus*, and *Scolytus ventralis*). An extended set of images for these three species with magnified sections and detailed measurements is reported in Supplementary Material 1. Correspondingly, Figure 2 contains representative examples of single- and multiple-noted calls of several key species from all tribes and all three stridulatory organs (see Supplementary Material 3 for all recorded species). These sound pressure level (SPL) spectrograms depict the variability found within these beetles in all measured spectro-temporal features.

Seven spectro-temporal call parameters (mean±sd) were estimated for all the recorded species (Table 2). *Dendroctonus frontalis, D. brevicomis, Scolytus ventralis, Platypus apicalis, P. gracilis*, and *Euplatypus parallelus* were the only species where both sexes

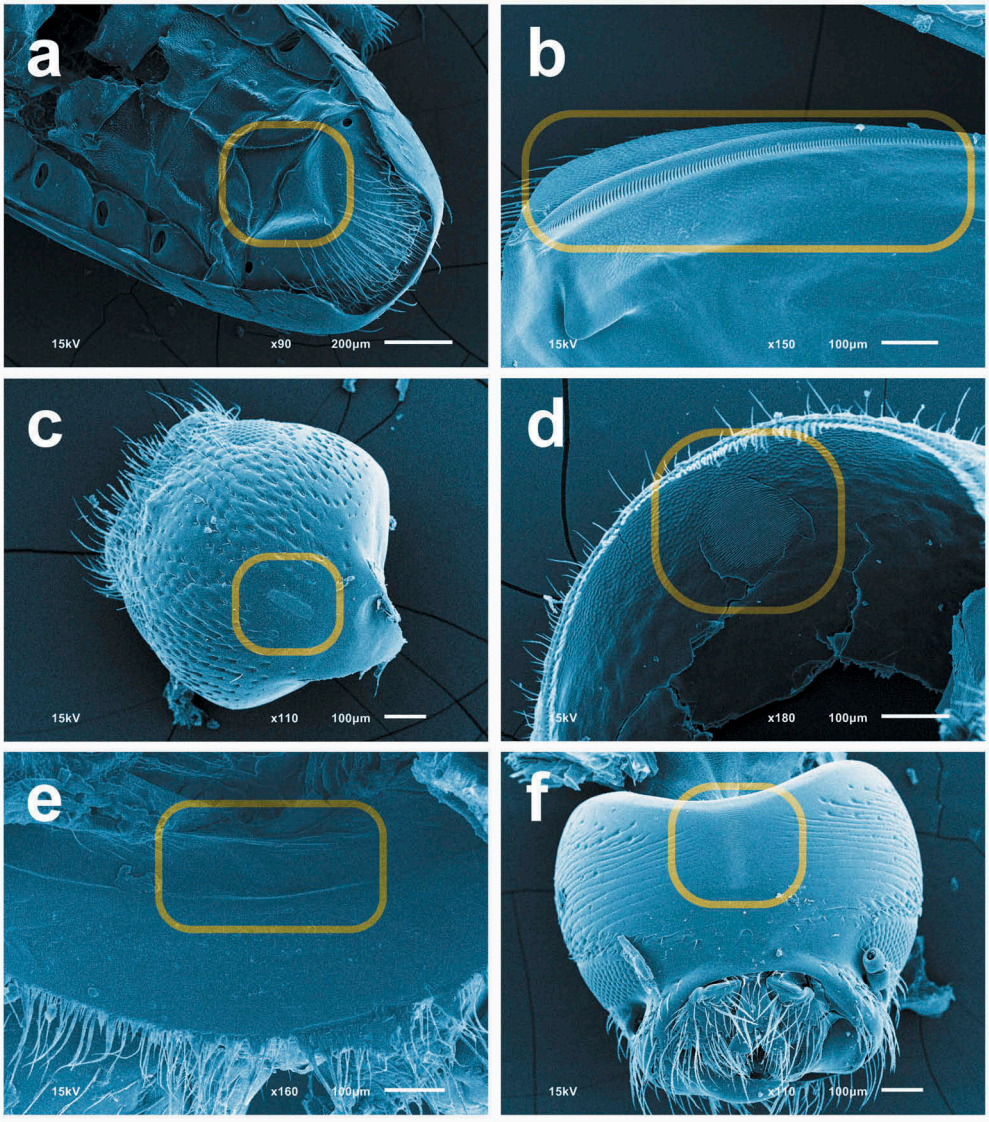


**Figure 1.** Scanning electron microscope images of the three main types of stridulatory organs (circled in yellow). (**a-b**) Elytro-tergal (*Euplatypus parallelus* male), (**c-d**) Vertex-pronotal (*Ips avulsus* female), (**e-f**) gula-prosternal (*Scolytus ventralis* male). Plectrum (left column – **a,c,e**) and pars stridens (right column – **b,d,f**). See Supplementary Material 1 for an extended set of images with close ups and measurement tags.

stridulated, whereby the sounds of males and females differed in all cases (Table 2 and Supplementary Material 3). Females of *E. parallelus* had the fastest calling rate, with 7.6 notes per second (nps) on average. In general, pinhole borers (Platypodinae) tended to stridulate louder than the bark beetles (Scolytinae) (Supplementary Material 3). Sounds of *P. apicalis*, were particularly loud and audible to the human ear up to 5 cm away from the gallery entrance (pers. obs.).

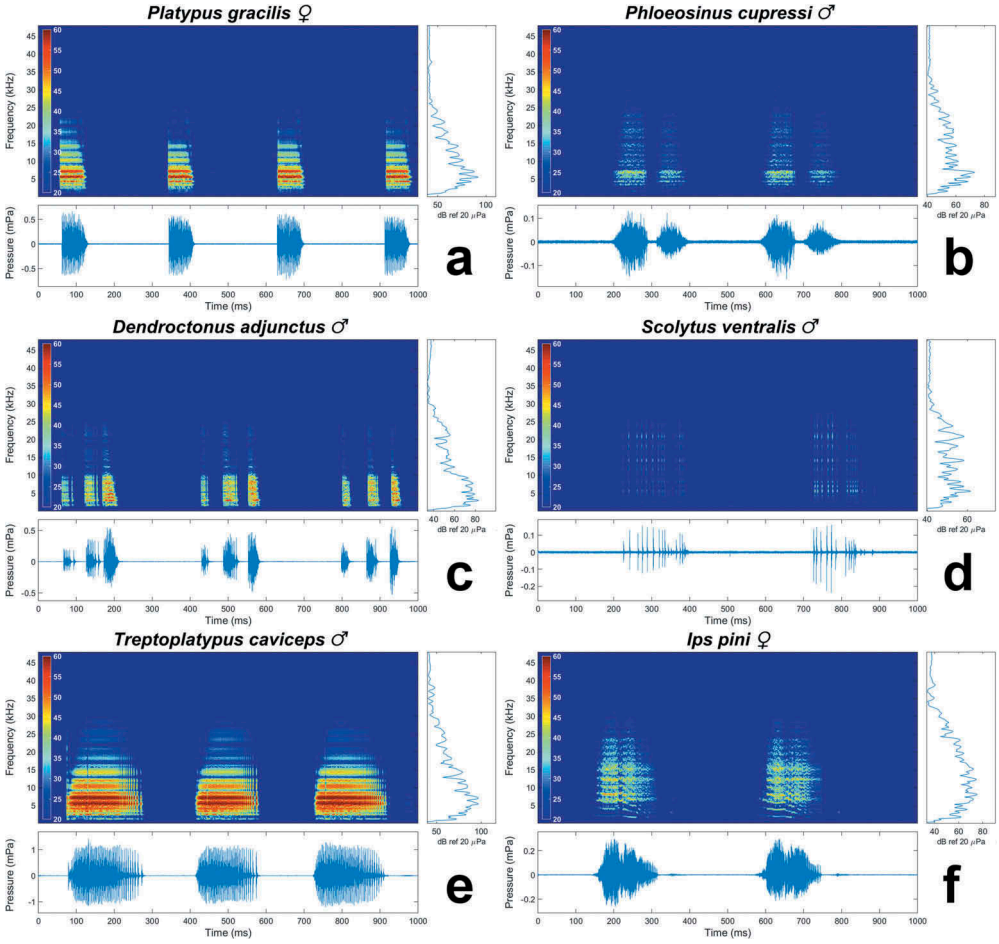


**Figure 2.** Sound pressure level spectrogram (top), time-domain representation (bottom), and sound pressure level spectrum (right) of representative bark and ambrosia beetle species. Colour bars in dB(SPL) ref 20 μPa. The figure depicts species whose calls have a different number of notes (**a,d,e,f** – one note, **b** – two notes, **c** – three notes), different stridulatory organs (**a,b,c,e** – elytro-tergal, **d** – gula-prosternal, **f** – vertex-pronotal), and represent different tribes (**b,c** – Hylesinini, **d,f** – Scolytini, **a,e** – Platypodini). See Supplementary Material 3 for the complete set of figures.

In general, sounds produced with vertex-pronotal and gula-prosternal organs had less intra-organ acoustic variability, both within and between species, compared with the elytro-tergal case (Table 2), which had highly variable spectral distributions and temporal patterns (Supplementary Material 3). This phenomenon can be observed in the species of the genus *Ips*, and males and females of *S. ventralis*, where stridulatory sounds are similar among themselves.

In five species, several acoustic morphotypes were identified (Table 3). When the call was composed of a single note, the temporal parameters of the note and call were the same (thus avoiding reporting inter-note intervals and note duration for all species, as these have been stated in Table 1; see Bedoya et al. (2019a) for an in-depth description of the notation). *Phloeosinus cupressi* was the only species whose stridulations were always

**Table 2.** Spectro-temporal features extracted from the acoustic dataset of beetles (mean±sd). **Sex** (gender with sound production capabilities), **Organ** (type of stridulatory organ, **E-T**: elytro-tergal, **V-P**: vertex-pronotal, **G-P**: gula-prosternal), **Dom** (dominant frequency), **Cen** (spectral centroid), **Min** (minimum frequency), **Max** (maximum frequency), **ICI** (inter-call interval), **Dur** (call duration), **CR** (calling rate; notes per second, nps) .

| | | | Spectral (kHz) | | | | Temporal | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Sex | Organ | Dom | Cen | Min | Max | ICI (ms) | Dur (ms) | CR (nps) |
| *Dendroctonus adjunctus** | ♂ | E-T | 5.94 ± 1.94 | 6.40 ± 0.58 | 2.99 ± 0.13 | 10.3 ± 1.68 | 188.5 ± 131.4 | 39.0 ± 12.2 | 4.5 ± 1.6 |
| *Dendroctonus brevicomis* | ♀ | E-T | 7.37 ± 3.18 | 8.69 ± 1.76 | 3.78 ± 1.10 | 16.8 ± 4.15 | 416.1 ± 405.7 | 36.1 ± 23.0 | 2.0 ± 1.0 |
| *Dendroctonus brevicomis* | ♂ | E-T | 6.03 ± 1.50 | 7.41 ± 1.02 | 3.86 ± 0.74 | 14.3 ± 4.21 | 531.7 ± 312.3 | 68.1 ± 27.4 | 1.5 ± 0.4 |
| *Dendroctonus frontalis* | ♀ | E-T | 7.99 ± 4.36 | 10.1 ± 2.98 | 3.74 ± 0.98 | 21.2 ± 5.53 | 226.7 ± 109.7 | 27.1 ± 06.5 | 3.7 ± 1.3 |
| *Dendroctonus frontalis* | ♂ | E-T | 7.62 ± 1.48 | 9.16 ± 1.42 | 3.85 ± 0.73 | 18.2 ± 3.84 | 184.5 ± 200.9 | 59.9 ± 19.2 | 4.7 ± 1.8 |
| *Dendroctonus pseudotsugae* | ♂ | E-T | 4.92 ± 1.25 | 5.26 ± 0.71 | 2.86 ± 0.42 | 8.16 ± 2.03 | 268.6 ± 158.2 | 36.4 ± 08.8 | 3.3 ± 0.5 |
| *Dendroctonus terebrans* | ♂ | E-T | 22.6 ± 6.05 | 22.2 ± 1.74 | 6.08 ± 2.23 | 39.2 ± 3.57 | 557.6 ± 066.7 | 99.3 ± 21.9 | 2.3 ± 1.1 |
| *Euplatypus parallelus* * | ♀ | E-T | 9.07 ± 2.90 | 13.1 ± 0.81 | 4.29 ± 0.70 | 27.1 ± 1.61 | 044.2 ± 084.0 | 42.9 ± 21.0 | 7.6 ± 6.4 |
| *Euplatypus parallelus* * | ♂ | E-T | 4.96 ± 1.06 | 6.02 ± 0.73 | 3.24 ± 0.47 | 10.1 ± 1.55 | 194.4 ± 130.9 | 37.2 ± 10.4 | 5.1 ± 3.5 |
| *Hylastes ater** | ♂ | E-T | 7.65 ± 1.66 | 8.51 ± 2.21 | 3.43 ± 1.18 | 13.8 ± 4.66 | 501.6 ± 333.1 | 98.4 ± 33.9 | 1.9 ± 0.2 |
| *Hylesinus aculeatus* | ♂ | E-T | 7.15 ± 2.20 | 9.05 ± 1.60 | 4.88 ± 0.75 | 19.4 ± 3.81 | 118.8 ± 102.7 | 29.5 ± 08.4 | 7.1 ± 1.1 |
| *Hylurgops subcostulatus** | ♂ | E-T | 5.44 ± 1.24 | 9.85 ± 0.73 | 4.09 ± 0.29 | 19.4 ± 1.34 | 338.8 ± 173.8 | 24.9 ± 02.7 | 5.2 ± 5.8 |
| *Hylurgus ligniperda* | ♂ | E-T | 7.90 ± 2.29 | 9.06 ± 1.98 | 3.48 ± 1.26 | 16.3 ± 4.92 | 150.5 ± 118.0 | 29.4 ± 13.6 | 4.5 ± 1.3 |
| *Ips avulsus* * | ♀ | V-P | 7.81 ± 3.40 | 11.5 ± 2.50 | 4.49 ± 1.38 | 24.5 ± 5.03 | 317.5 ± 324.0 | 73.7 ± 49.4 | 2.5 ± 1.2 |
| *Ips calligraphus* | ♀ | V-P | 13.3 ± 10.3 | 16.8 ± 6.24 | 4.53 ± 2.25 | 29.5 ± 8.76 | 138.8 ± 228.6 | 66.2 ± 53.5 | 4.9 ± 1.5 |
| *Ips grandicollis* | ♀ | V-P | 8.99 ± 6.34 | 12.2 ± 5.12 | 4.50 ± 1.64 | 23.8 ± 9.04 | 164.3 ± 282.9 | 59.6 ± 57.1 | 4.7 ± 1.8 |
| *Ips pini* | ♀ | V-P | 10.7 ± 4.74 | 12.8 ± 2.79 | 5.02 ± 1.88 | 22.6 ± 3.49 | 304.0 ± 301.7 | 63.9 ± 46.5 | 2.8 ± 0.6 |
| *Phloeosinus cupressi*†* | ♂ | E-T | 7.62 ± 2.67 | 9.42 ± 1.44 | 4.60 ± 0.71 | 16.9 ± 3.26 | 455.9 ± 379.0 | 179.4 ± 25.9 | 2.4 ± 0.7 |
| *Platypus apicalis* * | ♀ | E-T | 4.23 ± 1.46 | 5.10 ± 0.90 | 2.62 ± 0.35 | 9.12 ± 2.38 | 220.8 ± 145.9 | 20.7 ± 03.6 | 5.0 ± 1.1 |
| *Platypus apicalis* * | ♂ | E-T | 6.01 ± 1.81 | 6.68 ± 1.33 | 3.21 ± 0.68 | 11.3 ± 2.65 | 232.1 ± 148.4 | 40.2 ± 14.3 | 4.0 ± 0.9 |
| *Platypus gracilis* * | ♀ | E-T | 5.70 ± 0.49 | 6.48 ± 0.40 | 4.01 ± 0.41 | 10.9 ± 1.51 | 383.8 ± 328.7 | 54.8 ± 23.5 | 2.5 ± 0.9 |
| *Platypus gracilis* * | ♂ | E-T | 8.04 ± 2.55 | 8.22 ± 1.43 | 4.04 ± 0.63 | 13.5 ± 2.80 | 359.1 ± 171.2 | 75.8 ± 25.2 | 2.3 ± 0.3 |
| *Scolytus ventralis* * | ♀ | G-P | 6.03 ± 1.34 | 13.6 ± 3.06 | 3.43 ± 0.47 | 26.2 ± 8.07 | 111.5 ± 120.6 | 40.2 ± 21.5 | 4.9 ± 0.2 |
| *Scolytus ventralis* * | ♂ | G-P | 7.52 ± 4.17 | 10.6 ± 3.14 | 4.11 ± 1.05 | 22.9 ± 7.50 | 114.3 ± 141.2 | 35.1 ± 15.3 | 4.3 ± 2.2 |
| *Treptoplatypus caviceps** | ♂ | E-T | 5.76 ± 1.21 | 7.07 ± 0.63 | 3.57 ± 0.56 | 13.5 ± 2.93 | 414.1 ± 321.5 | 131.6 ± 40.7 | 1.7 ± 0.6 |

*Species for which calls are reported here for the first time; †*P. cupressi* has 2-noted calls whose acoustic parameters are reported in this table. For note parameters see Table 3. All other species have single-noted calls.

composed of 2-noted calls; thus, call parameters for this species are reported in Table 2, whereas the note parameters are in Table 3. *Dendroctonus adjunctus* was the only species with 3-noted calls. After the stimulus was applied, individuals of this species tended to adhere to a single acoustic morphotype for the whole stridulatory process, which lasted several minutes.

A PCA was performed to find general acoustic similarities among the studied bark and ambrosia beetle species (Figure 3). The two principal components with the largest eigenvalues explained 86.16% of the variability of the data: PC1 = 0.38Dom+0.19Cen-0.18Min-0.05Max-0.42ICI+0.72Dur-0.28CR contributed 46.85% and PC2 = 0.40Dom-0.34Cen-0.11Min-0.27Max-0.18ICI-0.16Dur+0.75CR the remaining 39.31%. The four species of the genus *Ips*, which only possess vertex-pronotal organs, were grouped into one cluster. Both male and female *Scolytus ventralis* significantly differed from the rest of the species and were part of the same compact cluster, possibly because of the gula-prosternal organ they possess. Most of the species with elytro-tergal structures, mainly composed of platypodines and *Dendroctonus* spp., clustered together. *Dendroctonus terebrans* was the biggest of the recorded species, and it was one of the species with the longest ICI, duration, and bandwidth (Table 2). Females of *E. parallelus* had the shortest ICI of all species and the fastest calling rate (Table 2, Supplementary Material 3), followed by *H. aculeatus* (Table 2). Both species were part of the same cluster. The rest of the species with elytro-tergal organs were grouped together (Figure 3).

## Discussion

A total of 55 bark and ambrosia beetle species were collected and their distress calls were examined, but only 33% of these stridulated. From these 19 stridulating species, seven spectro-temporal features were extracted and used for acoustic comparisons. This is the first report of acoustic signals for 11 of those 19 species, and both sexes stridulated in six of them. To contextualise, this is the largest acoustic dataset collected for the group, yet it does not even contain 1% of extant bark and ambrosia beetle species. When this information is combined with previous reviews of sound production (Barr 1969; Lyal and King 1996), the number of species investigated in this regard is still less than 2%. Furthermore, there is an evident bias in acoustic studies within the Scolytinae and Platypodinae favouring economically important species with sound production capabilities, and, with few exceptions (e.g. Barr 1969), absence of acoustic communication is not reported in the literature. This information is essential for understanding the acoustic diversity and the evolution of acoustic communication in the group, and we encourage other researchers to report absence of sound production.

**Table 3.** Temporal features for species with acoustic morphotypes with more than one note. **Sex** (gender with sound production capabilities), **NN** (number of notes), **INI** (inter-note interval), **nDur** (note duration)

| Species | Sex | NN | INI (ms) | nDur (ms) |
|---|---|---|---|---|
| *Dendroctonus adjunctus* | ♂ | 2 | 37.6 ± 09.6 | 37.9 ± 07.3 |
| *Dendroctonus adjunctus* | ♂ | 3 | 30.9 ± 08.7 | 35.0 ± 08.3 |
| *Dendroctonus frontalis* | ♂ | 2 | 18.4 ± 04.6 | 37.3 ± 12.1 |
| *Ips grandicollis* | ♀ | 2 | 23.3 ± 09.2 | 123.8 ± 59.3 |
| *Phloeosinus cupressi* | ♂ | 2 | 35.0 ± 25.7 | 100.5 ± 25.7 |

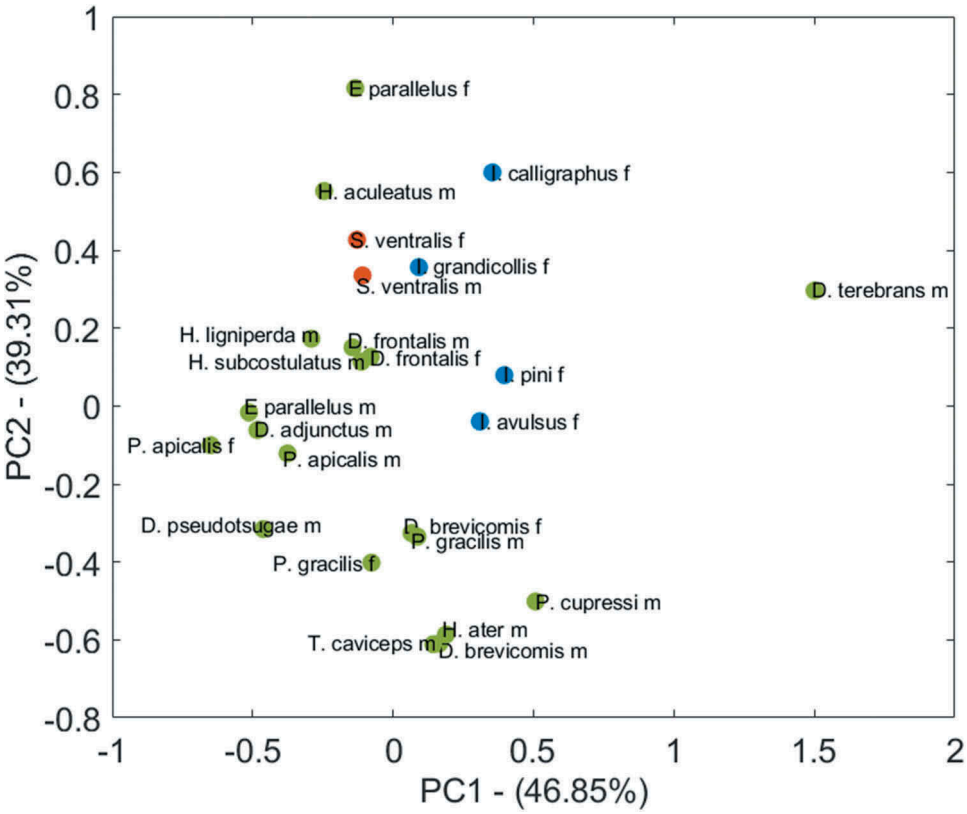


**Figure 3.** Principal component analysis performed on seven spectro-temporal features (dominant, centroid, minimum and maximum frequencies; call duration, inter-call interval, and call rate) of 19 bark and ambrosia beetle species. Colours represent different stridulatory organs (green: elytro-tergal, orange: gula-prosternal, blue: vertex-pronotal). The two principal components explained 86.16% of the variability of the data. Species with vertex-pronotal and gula-prosternal organs were grouped in compact clusters. With few exceptions, beetles with elytro-tergal organs tended to be together, although are sparsely distributed due to the interspecific variability of the sounds produced by this type of organ.

In species where both sexes stridulated, calls were acoustically different. This was expected, as sexual dimorphism in the stridulatory apparatus is common in Curculionidae (Barr 1969; Rudinsky and Michael 1973; Lyal and King 1996). Regarding intra-specific variation, the existence of several acoustic morphotypes has been reported previously in some bark and ambrosia beetle species (Fleming et al. 2013; Lindeman and Yack 2015). The variation of the number of notes in the call is possible due to the abdominal stretch-and-release mechanism (Lindeman and Yack 2019). In *D. adjunctus*, note length and note duration become shorter as the number of notes in the call increases, which coincides with the spring-loaded description of the elytro-tergal stridulatory movement reported by Lindeman and Yack (2019).

Our acoustic data collection was limited to the examination of a single behavioural context (i.e. distress/disturbance) due to three experimental and logistical reasons: (i) Bark and ambrosia beetles live inside plant tissue and colonise hosts with different acoustic

transmission properties that significantly affect the spectral parameters of the stridulations. This makes acoustic comparisons for all species unworkable in a behavioural context other than distress, as this is the only behaviour where sound production can be reliably controlled and elicited in a common medium (air). (ii) Acoustic data collection of bark and ambrosia beetles is difficult, as most species live and develop inside trees, and specimens must be collected alive, severely curtailing the use of funnel traps, and favouring the felling of trees, manual extraction from the wood, and the use of emergence chambers as the preferred course of action. The latter forms are particularly required for inbreeding polygynous species, where males are flightless and never leave the maternal chamber (Kirkendall 1983), and in economically unimportant species that are difficult to capture in traps because chemical lures are not available. For these reasons, we could only focus on a single behavioural context to maximise the number of species recorded, as testing other behaviours for all specimens would have added significantly to an already labour-intensive task. (iii) During the review of the literature, we found that among all bark and ambrosia beetle species where signals have been recorded and reported, distress sounds were always present in at least one of the sexes (Bedoya et al. 2019a,b; Hofstetter et al. 2019; Fleming et al. 2013; Lindeman and Yack 2015; Rudinsky and Vallo 1978; Rudinsky 1979; Vernoff and Rudinsky 1980; Yturralde and Hofstetter 2015). Nevertheless, the possibility that some species may have evolved acoustic communication in behavioural contexts other than distress is a limitation of our study. This is especially likely to occur in females, where presence or absence of acoustic communication is disputed in several species (Bedoya et al. 2019a; Rudinsky and Michael 1973; Ytsma 1988).

In behavioural terms, the acoustic responses to physical disturbances are well-known among the Scolytinae and Platypodinae (Bedoya et al. 2019a; Rudinsky et al. 1978; Ytsma 1988; Lyal and King 1996). The distress call is hypothesised to work as an agonistic sound to deter predators (Barr 1969; Ryker 1988), but no evidence for this hypothesis has been provided (Fleming et al. 2013). An alternative hypothesis is that it could work as a signal of non-agreement for copulation (e.g. when a male mistakenly mounts another male, as in the beetles of the genus *Rhynanchaenus* (Claridge 1968; Lyal and King 1996)).

Among the recorded Scolytini, *Ips avulsus* is the smallest *Ips* species (Wood and Bright 1992), and the smallest beetle (2.5 mm long) with sound production capabilities in our dataset. We were unable to find distress calls in either *Scolytus multistriatus* or *S. rugulosus*. On the other hand, in *S. ventralis*, both sexes stridulated, although less than 30% of the tested individuals (i.e. 9 beetles) responded to the stimulus. The genus *Scolytus* has a gula-prosternal stridulatory organ, which differs from the typical elytro-tergal organ found in most bark and ambrosia beetles (Barr 1969; Rudinsky 1979). Particularly, teeth separation in gula-prosternal organs tends to be wider than those of the elytro-tergal and vertex-pronotal organs (Barr 1969), which is a main contributor to the acoustic differences in the sounds the organ produce. Recent molecular phylogenies coincide in a basal separation of the subtribe Scolytina from the rest of the remaining members of the Scolytinae (Pistone et al. 2018), which partly explains the origin of the morphological differences in the stridulatory apparatus.

Among the recorded Hylesinini, *Dendroctonus adjunctus* was the only species able to produce distress calls consisting of three notes; nonetheless, specimens able to produce one and two notes per call were also found (see Supplementary Material 3 for the acoustic morphotypes). In this genus, females of *D. brevicomis* and *D. frontalis* lack the pars stridens

on the ventral surface of the elytra and the plectrum on the seventh abdominal tergite. Instead, the pars stridens appears to be located inside the posterior margin of the seventh sternum and the plectrum on the posterior margin of the eight tergite (Rudinsky and Michael 1973). Distress sounds have never been officially reported for any of these species; however, short-distance sounds in female-female interactions had been previously reported in *D. brevicomis* (Rudinsky and Michael 1973). For females of *D. frontalis*, sound production has never been reported in any behavioural context, although its existence has been suggested due to the presence of a similar stridulatory structure to the one present in *D. brevicomis* (Rudinsky and Michael 1973). The lack of detection of distress sounds by other researchers can be attributed to the type of stimulus applied, since females of these species do not stridulate when disturbed or 'pinched', even under life-threatening situations. However, they stridulate when touched with a soft brush on the ventral surface of the abdomen. Similarly, Rudinsky and Michael (1973) reported sound production by females in female-female interactions in *Dendroctonus pseudotsugae*, but we were unable to elicit distress sounds from females of this species. *Dendroctonus terebrans* was the largest of the collected species (with a length of 6.3 mm on average) and had the largest teeth separation in the pars stridens (Pajares and Lanier 1990), possibly explaining why its sounds did not resemble those of the other *Dendroctonus* species.

In 1988, Ytsma described the stridulatory apparatuses of most New Zealand platypodines (Brockerhoff et al. 2003) and provided anecdotal observational evidence of sound production for males and females of three species (*Platypus apicalis, P. gracilis* and *Treptoplatypus caviceps*), but stridulations were not recorded or reported. Here, we replicated most of Ytsma's findings, although we were unable to find sound production in females of *T. caviceps*, which responded neither to the distress stimulus nor to the sound-eliciting protocol described by Ytsma (1988). *Euplatypus parallelus*, the only American platypodine accessible to us, had several acoustic similarities with the New Zealand species, having elytro-tergal organs that produced loud and fast single-noted calls in both in males and females.

In contrast to the findings in Platypodinae, none of the ambrosia beetles in Scolytinae stridulated (i.e. *Gnathotricus* spp., *Monarthrum* spp., *Xyleborus* spp., *Xylosandrus* spp., *Xyleborinus saxesenii, Coccotrypes dactyliperda, Ambrosiodmus obliquus, Cnestus mutilatus*, and *Dryoxylon onoharaense*), and for this group we found no recorded signals in the literature. However, stridulatory-like organs which are thought to be sound-producing organs have been described in several xylomycetophagous scolytines (Barr 1969; Paiva and Kiesel 1985). We doubt that the feeding mode has any relationship with absence of sound production in these species, as xylomycetophagy is the norm in Platypodinae (Kirkendall 1983), yet they communicate acoustically. We also looked for sound production patterns in species with other feeding modes, but found no distress sounds in the two spermatophagous species examined (*H. hampei* and *D. longicollis*), although this sample size is too small to draw any reliable conclusions.

We found no stridulatory sounds among the inbreeding polygynous species in our dataset (i.e. *Xyleborus* spp., *Xylosandrus* spp., *Xyleborinus saxesenii, Hypothenemus* spp., *Ambrosiodmus obliquus, Cnestus mutilatus*, and *Dryoxylon onoharaense*). None of our xyleborines stridulated, and no species in the Xyleborina subtribe has ever been reported to produce sound. These species mate in the natal nest, where females are usually inseminated by their less numerous brothers (Kirkendall 1983). We hypothesise that in such a mating

system, acoustic communication plays a minimal role in mate-finding as the individuals live and reproduce in extremely confined environments and direct contact is almost unavoidable. Aside from this, we also found that none of the small species (< 2.5 mm) in our dataset stridulated, despite having closely-related species with sound production capabilities in the same genus (e.g. *P. dentatus*). Acoustic communication in insects is hypothesised to be morphologically restricted by size, as muscle power and sound rage tend to be proportional to the mass of the individual (Bennet-Clark 1998). The size of the smallest beetle with sound production in our dataset (*I. avulsus*, 2.5 mm) is similar to the sizes of the smallest insect species with sound production capabilities reported in the literature (i.e. *Drosophila melanogaster*, 2.7 mm; *Micronecta scholtzi*, 2.3 mm) (Sueur et al. 2011; Morley et al. 2018). Nonetheless, no empirical or theoretical size limits for acoustic communication have been determined. With the exception of a few outliers (e.g. *P. peregrinus*), mating system and size are enough to predict the presence or absence of acoustic communication in most of the recorded bark and ambrosia beetle species in this study. Nonetheless, this hypothesis, and the interaction between mating system and size, is something that needs to be tested with a larger dataset.

Species of the genus *Ips* were the only harem polygynous species in our dataset with sound production capabilities. These have a less common type of stridulatory organ (vertex-pronotal) than most bark and ambrosia beetles and only females stridulate (Barr 1969), suggesting a different evolutionary origin for acoustic communication in this taxon. This contrasts with previous reports of the polygynous genus *Polygraphus* where both sexes are able to acoustically communicate with elytro-tergal organs (Barr 1969; Lyal and King 1996). With the exception of the genera *Ips* and *Scolytus*, whose lineage was described above, the rest of the recorded species were monogamous and possessed elytro-tergal organs.

The most prominent result of the PCA (see also Supplementary Material 3) was the high diversity in sounds produced with elytro-tergal organs, which did not cluster together as they did with vertex-pronotal and gula-prosternal organs. This can be mainly attributed to the fact that 'elytro-tergal' is an umbrella term for a set of different stridulatory organs (Lyal and King 1996). In spite of being the most common type of sound-producing mechanism in weevils, the morphology and location of both the plectrum and pars stridens vary significantly across taxa (Lyal and King 1996). For instance, in the Platypodinae, the plectrum is located on the anterior part of the seventh abdominal tergite and the pars stridens is along the left elytral sutural flange (Ytsma 1988; Lyal and King 1996). Furthermore, the plectrum is sexually dimorphic and possesses inter-specific variability (Menier 1976; Ytsma 1988). In the Scolytinae, the plectrum is located on the posterior margin of the seventh abdominal tergite and the pars stridens is on the ventral surface of the elytron (Bedoya et al. 2019a; Barr 1969; Lyal and King 1996). The plectrum differs from that of the Platypodinae and, in most species, consists of a pair of tuberculiform processes (Lyal and King 1996). Aside from this, some genera, such as *Dendroctonus*, have inter-sexual differences in the stridulatory apparatus, where both plectrum and pars stridens are located in different parts of the body (Rudinsky and Michael 1973). Another factor expected to contribute to interspecific variability in bark and ambrosia beetle stridulations is morphology. Despite having a simplistic sound production mechanism (Lindeman and Yack 2019), species that share the same type of elytro-tergal organ will produce distinctive sounds due to differences in the spacing of teeth in the pars stridens, size of the plectrum, shape of the elytra, and speed of the ventral movement. These

morphological differences contribute to small interspecific differences in the estimated acoustic features that become more evident when all features are combined and analysed in multidimensional space.

Recent phylogenies refuting a close relationship between the Scolytinae and Platypodinae (Mugu et al. 2018), differences between the elytro-tergal organs of these subfamilies, and the absence of acoustic communication in closely-related groups to the Platypodinae (i.e. Dryophthorinae) suggest that acoustic communication has an independent evolutionary origin in these two subfamilies, and that this is a case of convergent evolution. Additionally, our data suggest that the type of mating system and beetle size play an important role in determining the acoustic communicatory capacity of most species. However, additional information is needed in order to make a strong case for the hypothesis that there are co-evolutionary patterns in mating systems, stridulatory-organs, and acoustic communication in bark beetles.

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