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REVIEW

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Acoustic communication in bark beetles (Scolytinae): 150 years of research

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Abstract

For over a century, the role of acoustic communication in the sensory ecology of bark beetles (Scolytinae) has been recognized. However, their 'world of sound' remains largely unexplored. Here, we review 153 years of bark beetle bioacoustics publications to summarize current knowledge, identify gaps and suggest future research directions. Our survey identified 117 publications covering 170 species. Morphological reports revealed five stridulatory organs across 125 species, with elytro-tergal, gular-prosternal and vertex-pronotum mechanisms being the most prevalent for sound production. However, confirmed sound recordings exist for only 40 species. Acoustic signalling in adults is proposed to function in avoiding enemies, pair formation, sexual selection and spacing, while in juveniles, vibratory communication is proposed for gallery spacing. However, experimental evidence supporting these functions is lacking. Acoustic sensory organs remain unidentified, and comprehension of signal transmission—whether through airborne sounds or solid-borne vibrations (or both)—is limited. Bioacoustic technologies have emerged as tools for potential management practices and are also discussed. Based on these findings, we recommend three directions for future research: (1) characterize acoustic morphology and behaviours in more species, particularly unrepresented taxa, with recordings in various contexts, preferably under natural conditions; (2) test hypotheses to explain the functions of acoustic communication through experimental and comparative phylogenetic methods and (3) investigate how sounds or vibrations are transmitted and received through behavioural and neurophysiological experiments. Advancements in bark beetle acoustic sensing and communication research will enhance our understanding of their sensory ecology and facilitate potential control measures of these fascinating insects.

KEYWORDS
behaviour, bioacoustics, Curculionidae, sensory, sound, vibration

INTRODUCTION

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are a large and diverse subfamily of weevils with significant economic, ecological and biological importance (Raffa et al., 2015). While some species are notorious pests of live-standing trees, others play crucial beneficial roles as primary decomposers, facilitating nutrient cycling and influencing forest landscapes (Raffa et al., 2015). Beyond the binary distinction of pests or non-pests, bark beetles have emerged as prominent research subjects for their diverse life cycles, mating and social systems (Kirkendall et al., 2015), population fluctuations and outbreak dynamics (Weed et al., 2015), their symbiotic associations with fungi and other microbes (Hofstetter et al., 2015) and chemical ecology (Raffa, 2001; Symonds & Gitau-Clarke, 2016). Given the broad scientific interest in these insects, a comprehensive understanding of their sensory ecology can provide crucial insights into how these insects interact with their environments and could inspire developments for acoustic technologies for management of pest species.

Bark beetles complete their life cycles both inside and outside of their host plants, where they use a variety of sensory modalities, including chemical, visual, tactile and acoustic, to interact with their environments (Campbell & Borden, 2006; Kerr et al., 2017). Most sensory ecology research has focused on chemical communication and sensing, particularly in the context of host selection (Andersson, 2012; Byers, 2007; Raffa et al., 2016). Acoustic communication and sensing are, in comparison, poorly understood. Previous reviews of the topic show that sound production is widespread throughout the subfamily and occurs in different behavioural contexts (Barr, 1969; Bedoya et al., 2021; Hofstetter et al., 2019; Lyal & King, 1996). Despite this, significant gaps persist in our understanding of which beetles produce sounds, how acoustic communication promotes survival and how acoustic signals are transmitted and received. We conducted a systematic literature review of acoustic sensory ecology in Scolytinae to understand the current state of knowledge and identify areas for future research. Here, we summarize what has been reported to date about sound production and sound-producing mechanisms and how these are distributed across various taxa, sexes and life stages. Furthermore, we review in which behavioural contexts acoustic signalling and sensing have been reported and consider hypotheses that might explain the functions of acoustic communication, as well as how signals are transmitted and sensed in natural environments. Lastly, we discuss the feasibility of using acoustic technologies in pest management and propose avenues for future research.

BARK BEETLE LIFE CYCLE AND SENSORY ECOLOGY

The term 'bark beetles' most commonly refers to species belonging to Scolytinae, a subfamily of ~6000 species within the true weevils (Curculionidae) that have lost their 'snout', and where adults and larvae have adapted to live most of their lives inside plant tissues (Kirkendall et al., 2015). Bark beetle adults have morphological characteristics well-suited for a tunnelling lifestyle, including a cylindrical body shape, strong mandibles and short antennae, which can be folded (Kirkendall et al., 2015). Note that sometimes the term 'bark beetle' is used interchangeably with 'ambrosia beetles'. However, 'ambrosia beetles' refers to species belonging to two subfamilies (Platypodinae and Scolytinae) that share similar characteristics due to convergent evolution (Hulcr et al., 2015). This review is confined to Scolytinae. However, species within Platypodinae have also been reported to produce sounds (Bedoya et al., 2021; Lyal & King, 1996; Ohya & Kinuura, 2001), making them a worthy subject for investigations of acoustic sensory ecology.

Bark beetle species show remarkable diversity in their life history traits, including their mating strategies, feeding and spacing patterns, associations with symbionts and degree of sociality (Kirkendall et al., 2015; Raffa et al., 2015). To illustrate the general life stages and sensory ecology of Scolytinae, we use the example of the mountain pine beetle *Dendroctonus ponderosae* Hopkins, 1902 (as reviewed in Fleming et al., 2013; Ryker & Rudinsky, 1976a; Safranyik & Carroll, 2006) (Figure 1). In *D. ponderosae*, the female is the pioneer (or colonizing) sex, which locates a host tree using visual and chemical cues (Figure 1a). The female initiates a gallery (Figure 1b) and may release 'aggregation' pheromones to attract conspecifics. Host colonization is eventually limited to prevent overcrowding by the release of 'anti-aggregation' pheromones by both sexes. The gallery entrance is blocked by the female to exclude conspecifics and enemies (Figure 1c). Upon arriving at the tree, a male approaches the gallery entrance (Figure 1c) and produces chirping sounds. If the male is accepted to the gallery, courtship and copulation occur, and during this process, signalling may be produced by both sexes (Figure 1d). After mating, the male assists the female in excavating the gallery and also guards the entrance to prevent other males from entering the gallery (Figure 1e). Males chirp during these rivalry encounters. Females lay eggs in separate niches along the gallery, and upon hatching, larvae feeding on the phloem excavate mines (tunnels) that radiate away from the parental gallery (Figure 1f). Beyond our knowledge of the acoustic sensory ecology of *D. ponderosae*, acoustic sensing and communication have been reported or proposed for a wide range of contexts in other species and these will be discussed in the Functions of Acoustic Communication and Sensing section of this review.

LITERATURE SEARCH

A literature survey was performed to identify primary research relating to bark beetle (Scolytinae) acoustic sensing and communication. Our process involved searching two databases (*Web of Science* and *Scopus*) including literature published between January 1945 and November 2022. The search was carried out with general keywords to identify a broad initial dataset using the following terms: 'Scolytinae' OR 'Bark beetles' OR 'Scolytidae' in mandatory combination with terms 'Sound' OR 'Vibration' OR 'Stridulation' OR 'Communication' OR 'Acoustic'. In addition, references cited from all English papers were searched in *Google Scholar* and when available, were added to our dataset. This additional procedure was performed to capture publications older than 1945, which is a limitation of *Web of Science* and *Scopus* databases. The initial dataset was further screened, and all publications that report acoustic recordings, morphology or behaviours shown or proposed to be involved in sound production were included in the final dataset. The final dataset includes peer-reviewed journal articles, reviews and book chapters but excludes

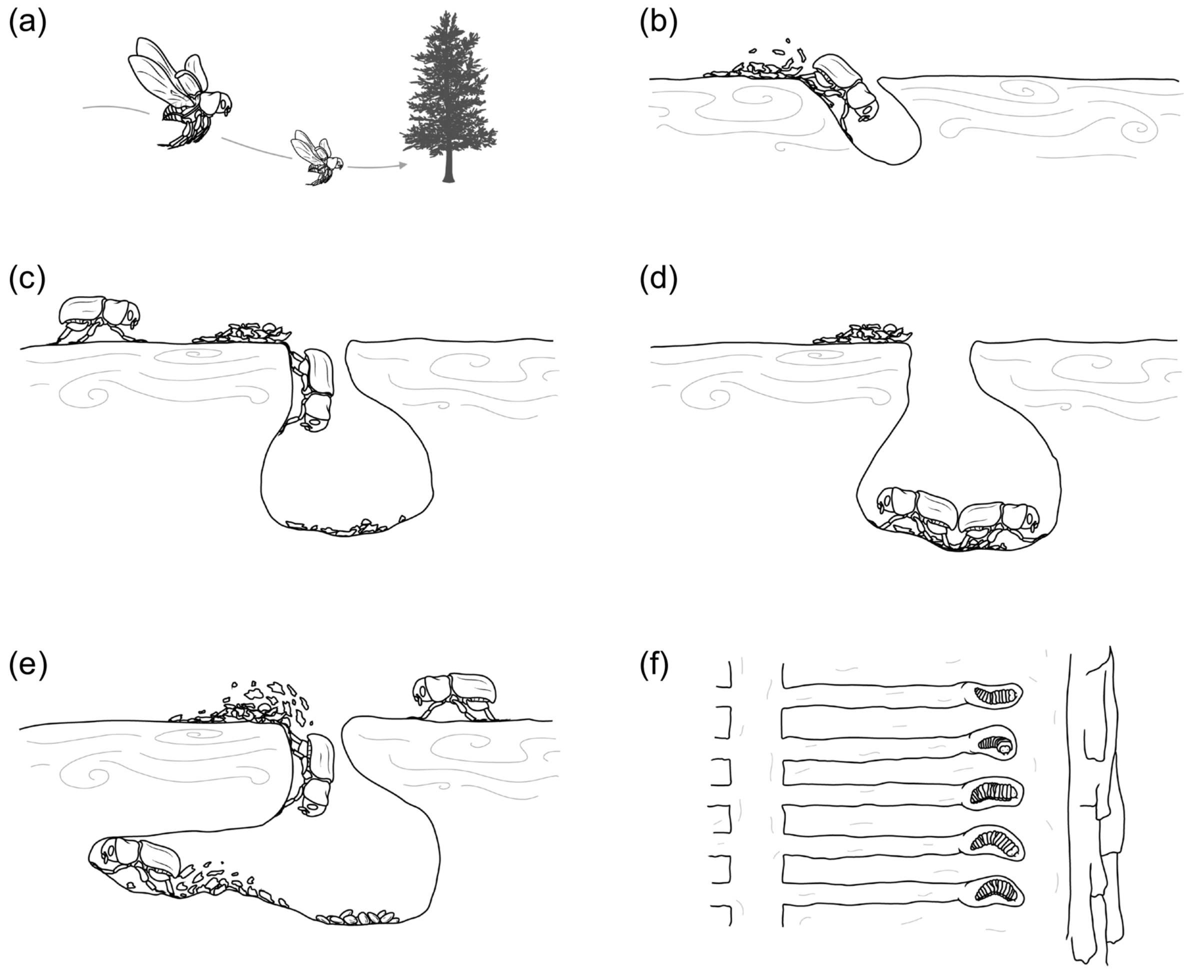

FIGURE 1 Generalized life cycle of the mountain pine beetle, *Dendroctonus ponderosae*. (a) Adult female (colonizing sex) locates a host tree; (b) female initiates a chamber; (c) female blocks the entrance to the chamber and male approaches; (d) male gains entrance to the chamber and the pair copulate; (e) male and female excavate egg gallery and remove frass; male may guard the entrance to prevent intruders, including other males, from entering the gallery. The female lays eggs in niches along the gallery (not shown); (f) larvae create individual feeding tunnels in the phloem and eventually pupate. Illustration credit: Kaylen Brzezinski.

duplicate references, technical reports, protocols, patents, editorials, theses and proceedings of meetings or conferences.

We identified 117 papers published between 1869 and 2022 that reported evidence for acoustic communication based on morphology, behaviour and/or sound recordings for at least one species of Scolytinae. The dataset was analysed to report on overall temporal trends in publishing, and major topics covered, including taxonomic groups (i.e. tribes, genera and species), types of stridulatory organs, behavioural contexts, life stages and sexes. This information was compiled and summarized in Table S1. According to our survey, scientific publication on bark beetle acoustics began in 1869 from the report of the physicist and naturalist Thomas Algernon Chapman who mentions a few species that 'squeak audibly' (Chapman, 1869). Notably, the studies exhibited slow linear growth until the early 1960s (<10 cumulative papers published) (Figure 2a). Afterwards, there was an exponential growth in publication output extending to the present (Figure 2a). Most papers focused on morphological features ($n = 112$ papers including overlaps) and/or behaviours shown or proposed to be involved in sound production ($n = 94$ papers including overlaps). Only half of the papers included acoustic recordings (referred to as 'Sound'; $n = 58$ papers including overlaps) (Figure 2a). From the 117 papers, a total of 14 tribes, 47 genera and 170 species of bark beetles were identified, with most papers focused on the tribes Hylurgini (47%), Ipini (19%), Polygraphini (7%) and Scolytini (6%). The remaining 21% of papers were distributed across 10 tribes (Figure 2b; Table S1). Further information on the taxonomic distribution of sound production is reported in a subsequent section of this paper.

ADULT BARK BEETLE ACOUSTICS

Sound production and mechanisms

At least five sound production mechanisms have been reported in Scolytinae: elytro-tergal (E-T), vertex-pronotum (V-Pr), gular-prosternal (G-Pr), pygidium-sternal (P-S) and elytro-tibial (E-Ti)

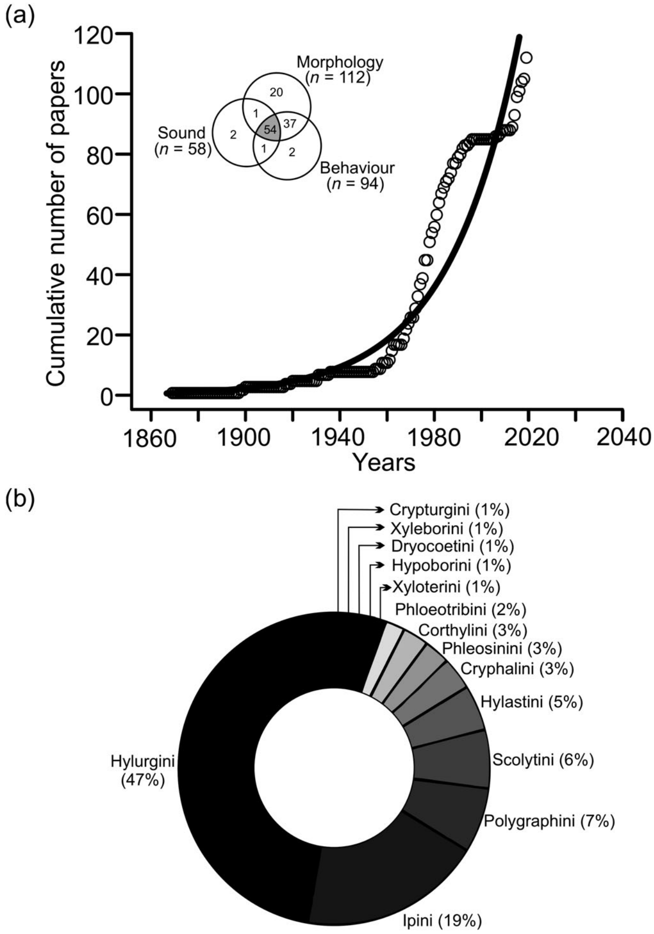

FIGURE 2 Summary of the bark beetle literature. (a) Cumulative number of papers (published between 1869 and 2022) with evidence for acoustic communication based on one or more of morphology, behaviour or sound recordings, for at least one species of Scolytinae. Most papers focused on morphological features ($n = 112$ papers including overlaps) and/or behaviours shown or proposed to be involved in sound production ($n = 94$ papers including overlaps). Only half of the papers included acoustic recordings (referred to as 'Sound' in the figure; $n = 58$ papers including overlaps); (b) the overall number and proportion of papers sorted by Scolytinae tribes. Most papers focused on the tribes Hylurgini (47%), Ipini (19%), Polygraphini (7%) and Scolytini (6%). The remaining 21% of papers were distributed across 10 tribes.

(Figure 3). These mechanisms are all stridulatory. In insects, stridulation typically involves two sclerotized body structures rubbing against one another (Low et al., 2021). File and scraper mechanisms are common in Coleoptera, whereby a plectrum, consisting of one or more sclerotized protrusions or a defined ridge, is rubbed against the pars stridens (sometimes called a file) comprising a series of fine parallel elevated ribs (sometimes called teeth; Wessel, 2006). The pars stridens is typically the more complex of the two structures (Barr, 1969). In this section, we describe the morphology, sound characteristics and processes involved in producing sounds. In the following section of this paper, we discuss how these mechanisms are distributed across taxa, sexes and life stages.

Before describing sound-producing mechanisms, we first introduce the bioacoustic terminology used in this review (Figure 4) (see Greenfield, 2002 for more in-depth descriptions of insect bioacoustic terminology). We use the terms 'sound' for airborne vibrations, 'near-field' and 'far-field' sounds to refer to the displacement and pressure components of airborne vibrations, respectively, and 'vibrations' for solid-borne vibrations. Sounds and vibrations are typically described by their temporal, spectral and amplitude characteristics (Figure 4). In the temporal domain, a sound pulse is the smallest indivisible unit (Broughton, 1963), and groups of pulses are variously named depending on the organism (Greenfield, 2002). In bark beetles, for instance, a variety of terms have been used to describe primary pulse groupings, including 'clicks', 'simple chirps', 'double chirps', 'multi-impulse chirps', 'major chirps', 'minor chirps', 'long chirps' and 'interrupted chirps' (Fleming et al., 2013; Rudinsky & Michael, 1973; Rudinsky & Ryker, 1976; Rudinsky, Vallo, & Ryker, 1978; Vernoff & Rudinsky, 1980). Inconsistencies in nomenclature could potentially lead to misunderstandings and hinder effective communication among researchers, and we recommend that, when possible, authors define pulse groupings using clearly defined criteria (Fleming et al., 2013; Lindeman & Yack, 2015). Figure 4 illustrates terminology used for describing temporal and spectral sound features that we refer to in this review, using the mountain pine beetle (*D. ponderosae*) as an example. Proper characterization of acoustic features requires specialized equipment to allow measurements across different frequencies and amplitudes and an understanding of how signals are transmitted in the insect's natural environment.

Elytro-tergal mechanism

E-T stridulation in bark beetles involves a plectrum (scraper) on an abdominal tergite and a pars stridens (file) on the posterior ventral surface of one elytron, usually the left (Figures 3a and 5) (Barr, 1969; Bedoya et al., 2021; Lyal & King, 1996). This is the most commonly reported sound production mechanism among the Scolytinae (Table S1). The morphology of this apparatus can vary between genera and species, and even within species, particularly in the number of ridges on the pars stridens and the shape and location of the plectrum (Barr, 1969; Lyal & King, 1996). Sounds produced by individuals with E-T structures have been described as clicks, simple chirps, multi-impulse and interrupted chirps (e.g. Lindeman & Yack, 2015; Rudinsky & Michael, 1973; Rudinsky, Oester, & Ryker, 1978; Ryker & Rudinsky, 1976b). Sounds are generated as the plectrum moves along the pars stridens (Figure 5). Distress signals generated by E-T are reported to be short in duration, ranging from 9.6 ms (Vernoff & Rudinsky, 1980) to 179.4 ms (Bedoya et al., 2021) with dominant frequencies between 1.5 kHz (Aflitto & Hofstetter, 2014) and 22.6 kHz (Bedoya et al., 2021).

E-T sounds, morphology and mechanisms have been best described in the red turpentine beetle, *Dendroctonus valens* LeConte, 1860 (Figure 5) (Lindeman & Yack, 2015, 2019; Michael & Rudinsky, 1972; Ryker & Rudinsky, 1976a). Males possess a pars

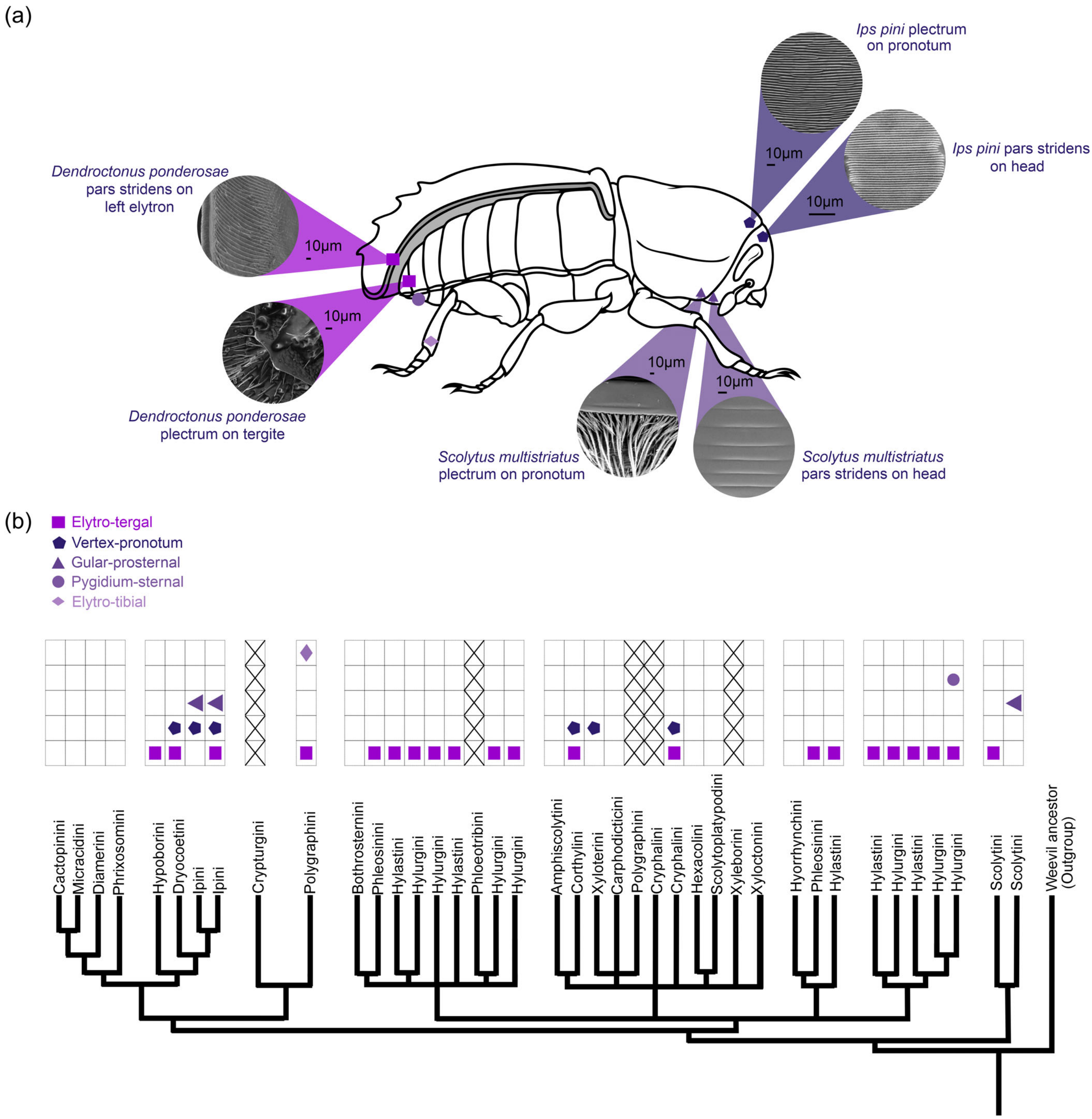

FIGURE 3 Sound production mechanisms in Scolytinae and their distribution across the 26 tribes. (a) Location of the five stridulatory organs (documented or proposed) in Scolytinae. The mechanisms are coloured according to the legend shown in part (b); scanning electron micrographs representing the pars stridens and plectrum are shown for the three primary mechanisms, from left to right (clockwise): elytro-tergal (male *Dendroctonus ponderosae*); vertex-pronotum (female *Ips pini*) and gular-prosternal (male *Scolytus multistriatus*). (b) Distribution of each stridulatory organ across the Scolytinae tribes. The phylogeny is drawn based on information obtained from Pistone et al. (2018). Boxes with an 'X' represent tribes for which at least one species has been examined but no stridulatory organ was found, and blank boxes represent tribes that have not yet been examined for the presence of acoustic mechanisms, to the best of our knowledge. All micrographs were provided by the Yack lab. Illustration credit: Kaylen Brzezinski.

stridens on the ventral posterior left elytron, and a plectrum comprising a pair of protrusions located on the seventh abdominal tergite (Lindeman & Yack, 2015, 2019) (Figure 5a–d,h–j). Chirps are produced when accumulated elastic energy results in the movement of the plectrum along the ridges of the pars stridens in a stridulatory mechanism called 'spring stridulation' (Lindeman & Yack, 2019) (Figure 5h–j). Chirps were categorized as 'simple' and 'interrupted' (Figure 5h–j) based on objective criteria. The number of sound pulses

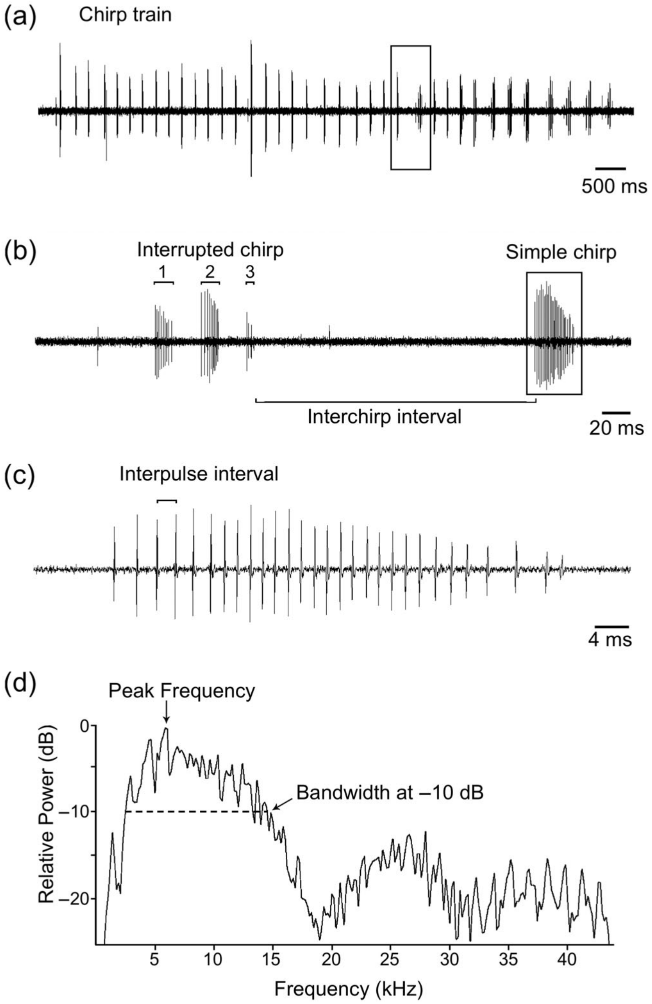

FIGURE 4 Acoustic characteristics of bark beetle sounds using a male mountain pine beetle (*Dendroctonus ponderosae*) as an example. (a) A chirp train in response to a disturbance. Box encloses two chirps that are shown in part (b). (b) An interrupted chirp showing three components (pulse trains) and a simple chirp showing one pulse train. Box encloses simple chirp shown in part (c). (c) Simple chirp from part (b) expanded to show individual sound pulses. (d) A representative power spectrum showing measurements used to describe spectral features. Adapted from Fleming et al. (2013), with permission.

per chirp correlates to the number of teeth on the pars stridens, with a simple chirp resulting from the plectrum moving along the pars stridens in a single movement in an anterior to posterior direction (Figure 5i) (Lindeman & Yack, 2019). Interrupted chirps are composed of a series of pulse groupings, called chirp components. During the production of interrupted chirps, the plectrum strikes the file ridges in one downward stroke, but in discrete intervals matching the number of the chirp's components (Figure 5j) (Lindeman & Yack, 2019). In the spectral domain, both simple and interrupted chirps (as recorded with a microphone) are broadband with bimodal peaks at ∼6 and 29 kHz (Lindeman & Yack, 2019). There is sexual dimorphism in the E-T structures (Figure 5a–g). Female *D. valens* has a pars stridens on the left elytron, but with fewer ridges and more shallow grooves between them (Lindeman, 2015) (Figure 5e), and the plectrum on the seventh abdominal tergite is absent (Lindeman, 2015; Lyon, 1958; Michael & Rudinsky, 1972) (Figure 5f). Female *D. valens* has been reported to produce sound in different contexts (Liu et al., 2020; Liu et al., 2017a; Liu et al., 2017b; Ryker, 1988; Ryker & Rudinsky, 1976b). While female *D. valens* lacks a plectrum on the seventh abdominal tergite, it is proposed that sounds are produced by using the chitinized posterior tip of the eighth abdominal tergite to strike the file ridges on the left elytron (Rudinsky & Michael, 1973; Ryker & Rudinsky, 1976b).

Vertex-Pronotum mechanism

The V-Pr stridulatory mechanism comprises two file-like structures—one on the dorsal surface of the head, called the pars stridens, and the other on the antero-ventral side of the pronotum, called the plectrum. As both are file-like structures, their designations as pars stridens and plectrum are arbitrary (Barr, 1969) (Figures 3 and 6). This is the second most commonly reported sound production mechanism in Scolytinae (Table S1). The morphology of the V-Pr varies among different species with respect to the shape, size and distance between ridges of both the pars stridens and plectrum (Barr, 1969; Sasakawa & Sasakawa, 1981). Sounds produced by V-Pr stridulation have been referred to as 'clicks', and 'interrupted', 'multiply interrupted' or 'uninterrupted' chirps (Oester & Rudinsky, 1975; Sivalinghem, 2011; Swaby & Rudinsky, 1976). Chirps are produced when the pars stridens (vertex on head) is rubbed against the plectrum (pronotum) as the head is moved posteriorly (Barr, 1969; Wilkinson et al., 1967). How the interaction of the pars stridens and plectrum relates to sound characteristics, such as the number of pulses, or chirp amplitude envelopes has not been assessed. Distress signals produced by the V-Pr mechanism are short in duration, ranging from 36 ms (Oester & Rudinsky, 1978) to 624.08 ms (Lewis & Cane, 1992) and dominant frequencies range between 750 Hz (Aflitto & Hofstetter, 2014) and 13.3 kHz (Bedoya et al., 2021).

Sounds produced by the V-Pr mechanism have been reported in several species of *Ips* (Table S1). We describe the sounds and proposed mechanisms in the pine engraver, *Ips pini* (Say, 1826) (Figure 6). Female *I. pini* have well-developed stridulatory structures. The pars stridens has many more ridges and less space between the ridges than does the plectrum (Figure 6a–e) (Dobai et al., 2018; Swaby & Rudinsky, 1976). Distress chirps are generated by the head moving posteriorly (not anteriorly) (Figure 6j) in agreement with the mechanism described for a congener, *Ips calligraphus* (Germar, 1823) (Wilkinson et al., 1967). Chirps produced by female *I. pini* display variability in both temporal and amplitude features (Figure 6h,i) and these features can vary between behavioural contexts (Dobai et al., 2018; Swaby & Rudinsky, 1976). To understand the mechanisms that contribute to this variability and whether females exert control over chirp features, further research utilizing high-speed video and acoustic analyses is necessary. In contrast to females, male *I. pini* lack file-like structures on both the head and pronotum (Figure 6f,g). While clicking

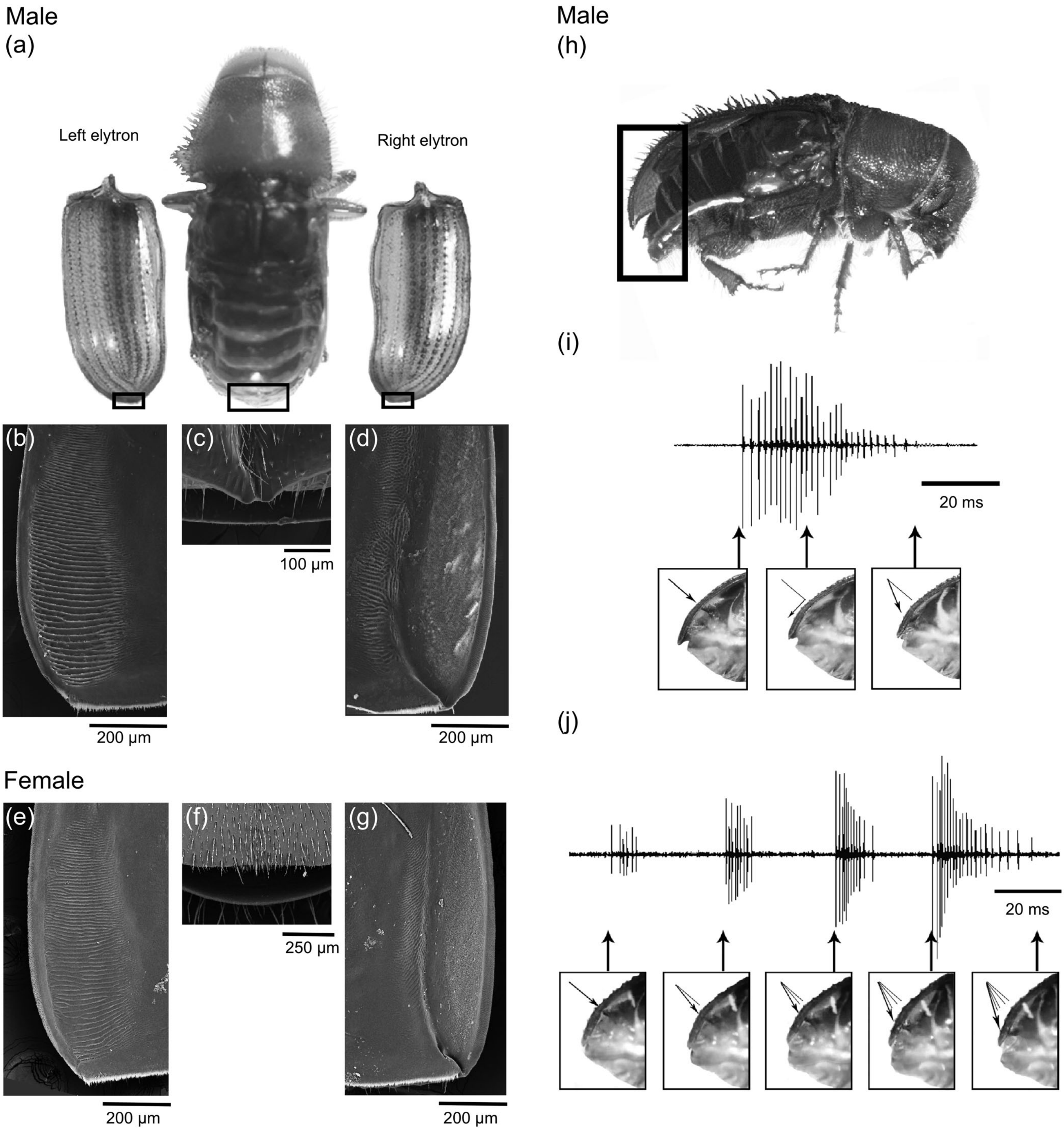

FIGURE 5 Elytro-tergal (E-T) stridulatory mechanism shown in the red turpentine beetle, *Dendroctonus valens*. In this species, the males are the primary sound producers. (a) Dorsal view of male *D. valens*, with both elytra removed and flipped over to show the ventral surfaces. Boxes show general locations shown in parts (b), (c) and (d), respectively. (b) Pars stridens on the left elytron of the male, showing the file ridges. (c) Plectrum located on the seventh abdominal tergite of the male. (d) Reduced file ridges on the right elytron of the male. (e) File on the left elytron of the female showing reduced ridges compared to the male. (f) Seventh abdominal tergite of female, showing lack of a plectrum in this region compared to the male. (g) Reduced file ridges on the right elytron of female. (h) Lateral view of a male with the right elytron removed to show region of the sound-producing mechanism. The general region of the plectrum and pars stridens is outlined in the box. (i) A simple chirp and video images showing movements of the plectrum during sound production. (j) An interrupted chirp with four chirp components, and video images showing the position of each component during sound production. All micrographs were provided by the Yack lab. Parts of this figure are adapted from Lindeman and Yack (2016), with permission.

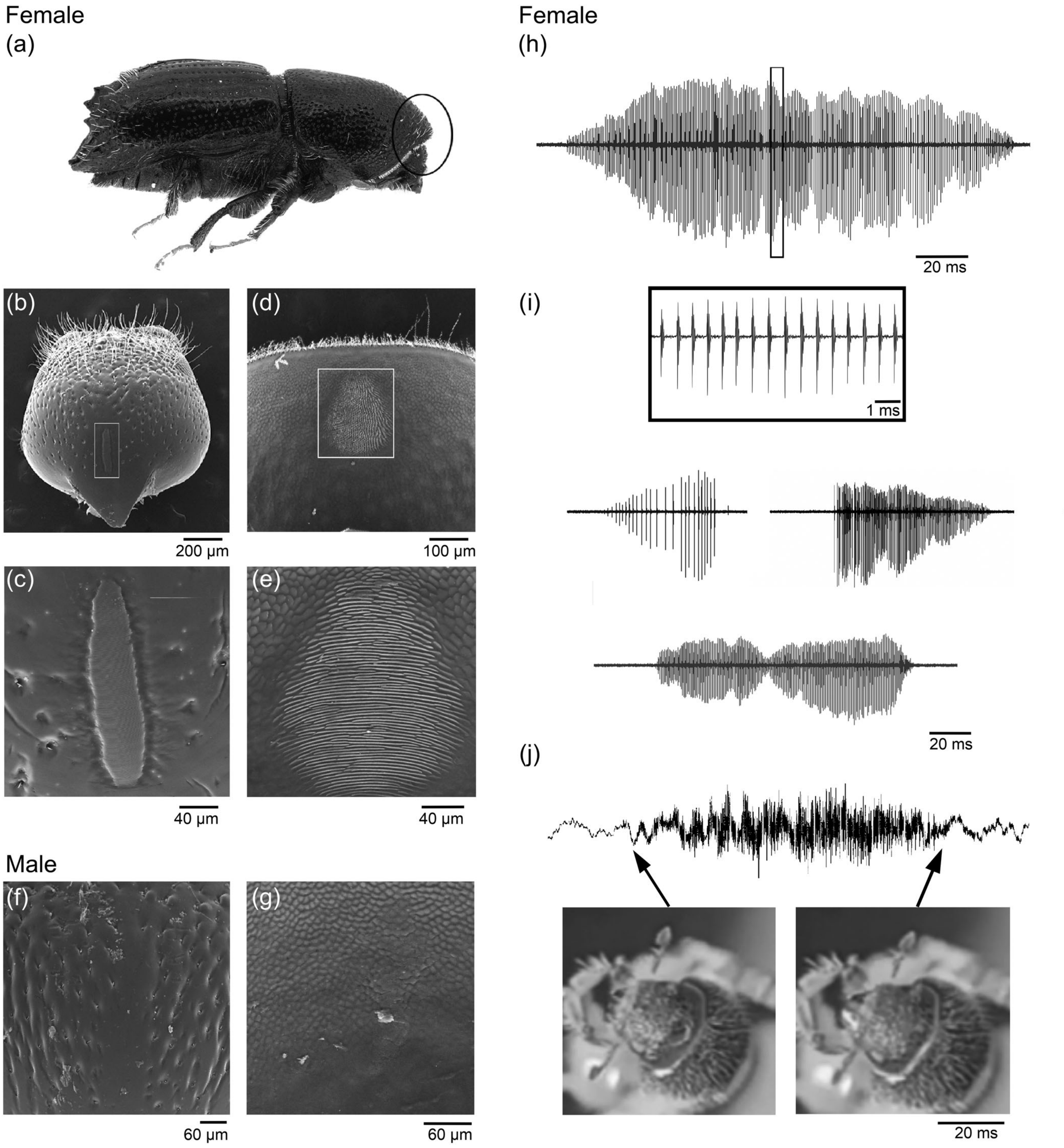

FIGURE 6 Vertex-pronotum (V-Pr) stridulatory mechanism shown in the pine engraver beetle, *Ips pini*. In this species, only the females are reported to make sounds using the V-Pr mechanism. (a) Lateral view of female with oval showing the location of the stridulatory organ. (b) Posterior view of the head in female. The box indicates where the pars stridens is located on the vertex of the head. This region is shown enlarged in part (c). (c) Enlarged pars stridens in female, as indicated in part (b). (d) Plectrum located on the ventral side of the anterior edge of the pronotum in the female. The box indicates the region where the plectrum is located. This region is shown enlarged in part (e). (e) Enlarged plectrum as indicated in part (d). (f) Enlarged view of the head region in the male showing lack of a pars stridens in the same general region shown for the female in part (c). (g) Enlarged view of the anterior edge of pronotum in the male showing lack of a plectrum in the same general region shown for the female in part (e). (h) Typical female chirp. Box encloses the region expanded below, which shows individual sound pulses. (i) Female chirps that show variation in durations and amplitude envelopes. (j) A single chirp showing corresponding head locations at the beginning and end of the chirp. This shows how the pars stridens on the head moves posteriorly across the plectrum on the inner surface of the pronotum to produce sound. All micrographs were provided by the Yack lab. Parts of this figure are adapted from Dobai et al. (2018), with permission.

sounds have been reported for males, the mechanisms are not known (Oester & Rudinsky, 1975).

Gular-Prosternal mechanism

The G-Pr mechanism is characterized by a file-like structure, the pars stridens, comprising transverse ridges running along the midline of the 'gula' (underside) of the head, as well as a single ridge, the plectrum, located on the ventral anterior edge of prosternum (Barr, 1969) (Figure 3). While Scolytinae are characterized by the presence of a 'pregular sclerite' (Wood, 1973), the term 'Gula(r)-prosternal' is commonly used (Barr, 1969; Jefferies & Fairhurst, 1982; Oester & Rudinsky, 1975; Rudinsky, Vallo, & Ryker, 1978). This stridulatory mechanism is the third most frequently reported in bark beetles (Table S1). Sounds have been referred to as 'interrupted chirps', 'clicks' and 'paired or double' chirps (Oester & Rudinsky, 1975, 1978; Rudinsky, Vallo, & Ryker, 1978). Chirps are produced when the ridges of the pars stridens on the head rub against the plectrum on the prosternum, as the head is nodded in an anterior–posterior direction (Barr, 1969; Rudinsky, Vallo, & Ryker, 1978). Distress sounds produced by the G-Pr mechanism range from 21.9 ms (Rudinsky, Vallo, & Ryker, 1978) to 134 ms (Oester & Rudinsky, 1978) with dominant frequencies ranging between 6 and 7.52 kHz (Bedoya et al., 2021).

Sounds produced by G-Pr mechanisms have been best described in two species: *Scolytus mali* (Bechstein, 1805) and *Ips concinnus* Wood & Bright, 1992. In *S. mali*, both sexes possess a well-developed G-Pr organ and both produce sounds in various contexts (Rudinsky, Vallo, & Ryker, 1978). Sounds are referred to as double chirps because two pulse groups occur as the head moves in an upward and then downward direction, respectively. Sexual dimorphism is reported in both the G-Pr morphology and chirp characteristics. The number of sound pulses per chirp in both sexes is lower than the number of ridges on the pars stridens, suggesting that not all the ridges are used in sound production (Rudinsky, Vallo, & Ryker, 1978). In *I. concinnus*, both males and females are reported to possess a G-Pr stridulatory organ and chirping in various contexts (Barr, 1969; Oester & Rudinsky, 1975, 1978). Chirps are produced by the movement of the head in a single rapid upward and forward motion and also as the head is moved slowly in an anterior–posterior motion (Oester & Rudinsky, 1975). Sounds have been described as chirps and clicks, but no paired or double chirps were reported for this species. Like for *S. mali*, the number of sound pulses per chirp in both sexes is lower than the number of ridges on the pars stridens, suggesting that only part of the pars stridens is being used, at least in the contexts studied (Oester & Rudinsky, 1978).

Other proposed mechanisms

Other sound-producing mechanisms have been reported for Scolytinae, including E-Ti and P-S structures (Figure 3; Table S1). An E-Ti stridulatory organ in male *Polygraphus proximus* Blandford, 1894 consists of transverse ridges on the costal margin of the elytron (pars stridens) and large spines on the inner surface of the hind tibiae (plectrum) (Kerchev, 2015, 2019). Males are described to produce chirps by rapidly bending and straightening their hind legs along the outer margins of the folded elytra. This behaviour was observed only prior to copulation (Kerchev, 2019). Recording sounds simultaneously with videos of body movements or ablating the spines on the tibiae would help to confirm this mechanism. Rudinsky and Michael (1973) proposed a new stridulatory organ in six female *Dendroctonus* species. We have called this a P-S structure based on the location of the proposed pars stridens, a series of ridges on the inside wall of the posterior margin of the last abdominal sternite and the plectrum, which comprises the posterior half of the eighth abdominal segment (the pygidium). It is reported that the tip of the plectrum strikes the pars stridens in a backward and downward motion. Sounds produced with P-S are called clicks and chirps and were recorded from females in the absence of males (Rudinsky & Michael, 1973). Stridulation using this mechanism was tested by covering the pars stridens on the sternum with glue, which prevented the chirps. Simultaneous sound recordings with video of body movements would help to confirm this mechanism of sound production.

TAXONOMIC DISTRIBUTION AND EVOLUTION OF SOUND PRODUCTION

The subfamily Scolytinae has ~6000 described species belonging to 247 genera and 26 tribes (Kirkendall et al., 2015; Pistone et al., 2018). Based on our literature survey, 14 of the 26 tribes are reported to include at least one species that exhibits evidence for acoustic communication based on morphology, behaviour and/or sound recordings; 2 of the 26 tribes (Crypturgini and Xyleborini) are reported to have no stridulatory organs and 10 of the 26 tribes have not been examined to date (Figure 3; Table S1). At present, acoustic communication evidence has been explored in only 3% of bark beetle species (170 out of 6000) representing 14 tribes and 47 genera. Of these, the presence of stridulatory organs was reported in 12 tribes, 33 genera and 125 species, and there are sound recordings for only 7 tribes, 13 genera and 40 species. Thus, while our results show that sound production is widespread across the Scolytinae, the vast majority of species and major taxa have not been examined to date (Figure 3b).

The five stridulatory mechanisms identified in our survey have a wide taxonomic distribution with unequal occurrence across the Scolytinae phylogeny (Figures 3b and 7; Table S1). The E-T is the most widespread, occurring in 11 tribes, 28 genera and 84 species. This mechanism occurs primarily in males; although, it is also reported to occur in females in some species (Table S1). The V-Pr is reported in 5 tribes, 6 genera and 27 species (Figures 3b and 7; Table S1). This mechanism is reported primarily in females, and in particular for *Ips* species (Table S1). The G-Pr mechanism is reported in 2 tribes (i.e. Scolytini and Ipini), 4 genera and 17 species (Figures 3b and 7; Table S1) and shown to occur in both sexes (Table S1). The two less known stridulatory mechanisms, E-Ti and P-S, are limited to

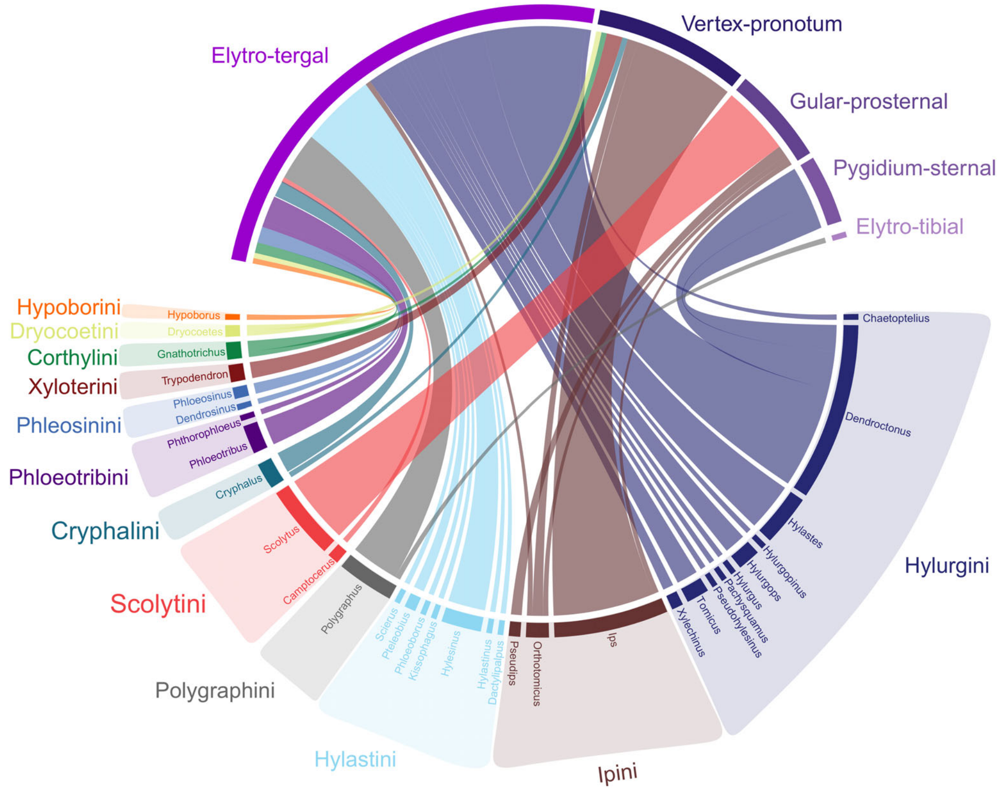

FIGURE 7 Interaction between the taxonomic groups (tribe and genus) and the five reported stridulatory organs across the Scolytinae tribes ($n = 12$) and genera ($n = 32$). Elytro-tergal is the most widespread mechanism occurring in 11 tribes and 28 genera. Vertex-pronotum is the second most reported mechanism occurring in five tribes and six genera. Gular-prosternal is reported in only two tribes and four genera. The two less known stridulatory mechanisms, elytro-tibial and pygidium-sternal, are limited to only two tribes, Polygraphini (one genus and one species) and Hylurgini (one genus and seven species), respectively.

Polygraphini (one genus and one species) and Hylurgini (one genus and seven species), respectively (Figures 3b and 7; Table S1). The E-Ti mechanism is reported to occur only in males (Table S1), while the P-S mechanism is reported to occur in only females.

Our literature review revealed some uncertainties regarding the occurrence and distribution of sound-producing organs in certain species. While most documented species are reported to possess a single stridulatory organ (Table S1), other species, including some *Dendroctonus* spp., *P. proximus*, *Cryphalus fulvus* Niisima, 1908 and *Dryocoetes autographus* Eichhoff, 1864, are reported to have more than one sound-producing organ based on their morphological characteristics (Table S1). Another issue refers to discrepancies in reports from different authors regarding the mechanisms present in the same species (e.g. *Gnathotrichus retusus* Wood & Bright, 1992, *C. fulvus*, *D. autographus* and *Orthotomicus angulatus* Wood & Bright, 1992) (Table S1). Additionally, uncertainties remain regarding which sex possesses the organ and whether these organs are capable of sound production (e.g. Barr, 1969). Moving forward, we recommend that when studying any species in the future, researchers examine all body parts in both sexes and attempt sound recordings in as many behavioural contexts as possible. Ablation methods may be necessary to provide a better understanding of the mechanisms involved, particularly in cases where multiple organs are present.

In summary, our survey highlights the prevalence and diversity of acoustic communication within the Scolytinae, with at least five sound-producing mechanisms distributed across several tribes and sexes. This diversity raises a series of compelling questions that require further investigation: How did these various mechanisms originate, and why did multiple mechanisms evolve within this group? Is there evidence for convergent or divergent evolution of different mechanisms? What factors determine why certain species and sexes produce sounds while others do not? To address these questions, comparative phylogenetic methods could be employed to test hypotheses explaining the evolution and diversity of acoustic communication.

FUNCTIONS OF ACOUSTIC COMMUNICATION AND SENSING

Bark beetles are reported to use acoustic signals in many different contexts, including anti-predator defence, mating, rivalry, colonization, gallery construction and spacing (Table S1). While signal functions are often implied based on their descriptors (e.g. 'attraction chirps', 'rivalry chirps' and 'stress chirps') (Swaby & Rudinsky, 1976), the adaptive value of signalling in any particular context has often

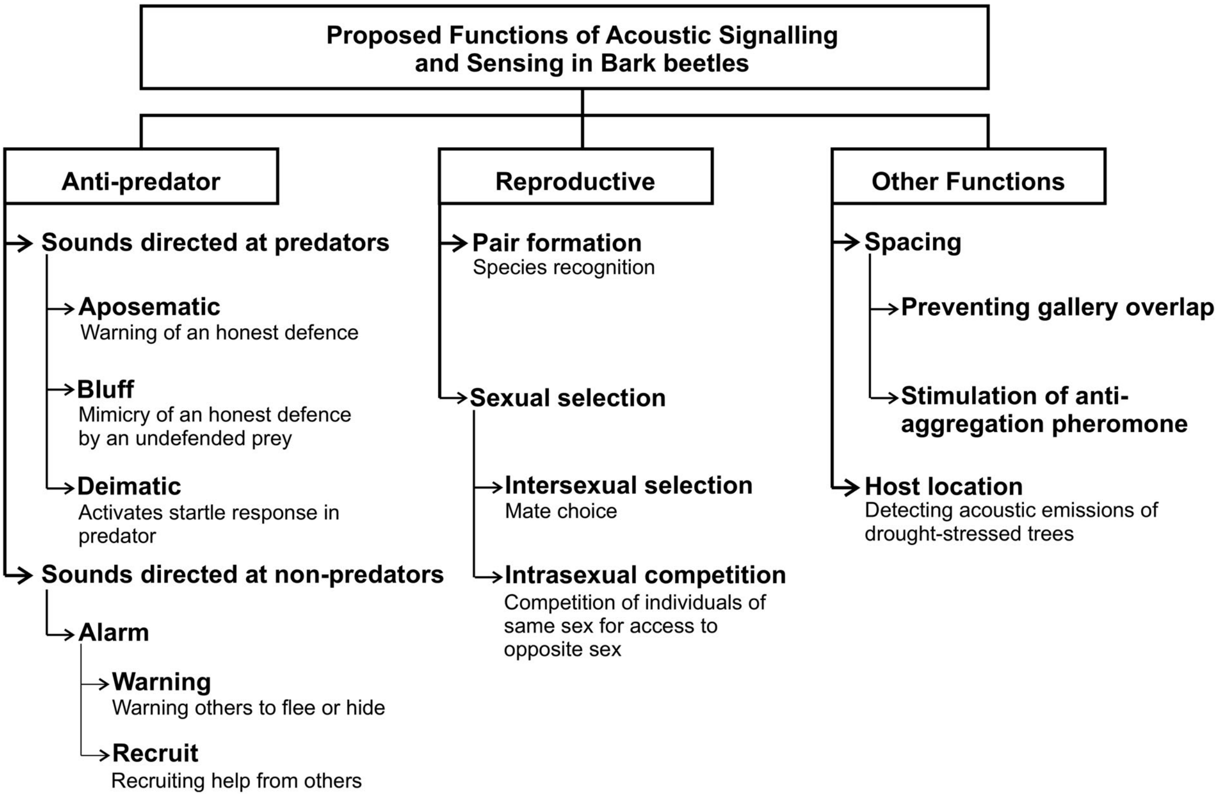

FIGURE 8 Hypotheses explaining possible functions of acoustic signals and sensing in bark beetles.

not been tested. Acoustic communication is thought to be a dominant form of communication for Scolytinae during close-range encounters inside the plant tissue, where visual communication is limited. However, studying behaviours and very low amplitude acoustic signals while beetles interact inside plant material is challenging, due to the technical limitations of acoustic and video equipment. Nonetheless, many studies have been conducted, which allow us to narrow down hypotheses on signal functions. Here, we consider hypotheses under three broad categories: antipredator, reproductive behaviour and other functions (Figure 8). Note that because we do not yet know how bark beetles transmit or detect acoustic signals, we generally refer to acoustic signals and events as 'sounds', even though transmission and detection may be via solid-borne vibrations.

Antipredator

Most sounds reported for Scolytinae have been those evoked by human holding, light pinching, probing or touching, a standard practice to test for sound production (Barr, 1969; Bedoya et al., 2021; Dobai et al., 2018; Vernoff & Rudinsky, 1980), and such sounds are often called 'stress', 'distress' or 'disturbance' chirps (Table S1). The survival value of such signals remains largely untested; however, an antipredator function has been considered (Dobai et al., 2018; Hofstetter et al., 2019; Kirkendall et al., 2015; Lewis & Cane, 1990). In insects, anti-predator sounds are defined as those produced in response to attack or threat of attack and ultimately promote the survival of the signaller (Low et al., 2021). Because pinching or probing by a human could be considered to be a 'simulated' predator attack, this provides indirect support for the antipredator hypothesis. However, experiments testing the selective advantage of such sounds in a natural context are lacking. Antipredator sounds in insects can be broadly categorized as those directed at predators, or those directed at non-predators (Low et al., 2021) (Figure 8). Signals directed at predators can, among other things, function to warn the predator of an honest defence (aposematism), dishonestly mimic an honest defence (bluff) or activate the startle response (deimatic display) (Low et al., 2021). Signals directed at non-predators could function as alarm calls to warn others or recruit help (Low et al., 2021).

Do bark beetles produce sounds directed at predators? As a first step in testing this hypothesis, experiments documenting predator–prey interactions while recording sounds are necessary to correlate prey acoustic behaviour with predator responses. There are few such studies in bark beetles. *Ips pini* female individuals were shown to produce chirps when attacked by a clerid beetle, *Thanasimus dubius* (Fabricius, 1777), in a petri dish (Dobai et al., 2018; Sivalinghem, 2011). While female chirps were recorded in response to predator attacks, the adaptive value of signalling was not resolved, as there was no support that the predator dropped or increased handling time in response to signalling females. In other studies involving predator–prey interactions, there is only indirect evidence for sound functioning as an antipredator defence, as sounds were not recorded. Lewis and Cane (1990) exposed female (noted to stridulate) and male (noted to be silent) *I. calligraphus* to *T. dubius* predators in a petri dish. The results showed that predators took longer to handle females than males and that the predator released females more frequently than males during the handling period. The authors also note that females stridulated vigorously during the handling period; although, the sounds were not recorded or directly correlated with the predator's response. Eventually, all prey were consumed by the predator. The authors proposed that sounds function as deimatic displays, which, in a natural context on a vertical bark surface, could cause the predator to drop the prey, facilitating the escape of the latter. We propose that, alternatively, signals could advertise overall fitness, informing the predator that the prey is unprofitable to pursue. In a fascinating anecdotal report suggesting a mimicry function, Wood (2007) describes the simultaneous stridulation of 100 or more adult *Dendrosinus bourreriae* Schwarz, 1920 in response to a disturbance of a tree limb where the beetles were burrowed and describes the sounds as 'giving the impression that the limb was infested by a swarm of angry bees'. Based on these studies, 'distress signals' in bark beetle adults may be targeting predators and may function to warn, startle or bluff their attackers.

Alternatively, could 'distress' sounds in bark beetles be directed at conspecifics? In insects, such sounds produced in an antipredator context can function as alarm signals to warn others to escape, to recruit help or even to attract competing consumers (Low et al., 2021). In bark beetles, some support for the 'warning conspecifics' hypothesis is provided in a study by Aflitto and Hofstetter (2014) where *Dendroctonus frontalis* and *Dendroctonus brevicomis* LeConte, 1876 were less likely to enter logs when conspecific 'stress calls' were played. However, stress calls did not reduce entry for another species, *I. pini*. Given that many bark beetle species live in social groups of varying complexity, often with genetically related individuals (Kirkendall, 1983; Kirkendall et al., 2015), communicating risk using acoustic signalling is a distinct possibility and should be further investigated.

To further test the hypothesis that bark beetle sounds function in an antipredator context, we recommend conducting experiments with natural predators, as well as playback studies. Bark beetles have many natural enemies, but perhaps those most relevant to our discussion of defence sounds are carnivorous beetles, such as the checkered beetles (Cleridae) and woodpeckers (Wegensteiner et al., 2015). Future studies should include interactions with predators while recording behaviours and sounds and these experiments should evaluate the responses of predators to sounds and the survival outcomes of prey based on their sound-producing capabilities. Playback studies of conspecific 'distress' sounds could be informative in testing the alarm signal hypothesis, by assessing if conspecifics exhibit positive or negative phonotactic responses. Alternative hypotheses for 'distress' sounds should also be considered, including the possibility that they may not function to deter or avoid predators at all, but function in other contexts in response to rivals or crowding.

Reproductive behaviour

Acoustic communication in the context of reproduction can occur from the time a potential mate approaches a gallery to post-copulation (e.g. Ryker & Rudinsky, 1976a) and plays an important role for many Scolytinae species (Table S1). Sounds produced in this context have been called, among other things, 'agreement', 'attractant', 'greeting', 'premating', 'courtship' and 'rivalry' signals (Rudinsky & Ryker, 1976; Ryker, 1988; Ryker & Rudinsky, 1976a, 1976b; Swaby & Rudinsky, 1976), implying different functions. Currently, however, the adaptive value of these signals is not well understood for bark beetles. The functions of reproductive signalling are most likely diverse, reflecting the wide diversity of mating systems, including various types of outbreeding (e.g. monogamy, polygyny), inbreeding and parthenogenesis (Kirkendall, 1983; Kirkendall et al., 2015). While many species exhibit sexual dimorphism of stridulatory organs, others do not (Barr, 1969; Bedoya et al., 2021). In those species exhibiting acoustic sexual dimorphism, sound production is noted to be less well developed or absent in the 'colonizing' sex (i.e. the sex that initiates gallery construction), which can be either male or female, depending on the species (Barr, 1969). Bedoya et al. (2021) suggest that the type of mating system may predict sound production capabilities. For example, species that lack sound production are more likely to participate in inbreeding (Bedoya et al., 2021). Here we summarize the literature relating to reproductive functions of acoustic communication under two broad and non-mutually exclusive hypotheses: pair formation and sexual selection (Figure 8).

Pair formation

The attraction and identification of potential partners are initial steps in the mating sequence of sexually reproducing insects, and some have evolved acoustic signals with a primary function of facilitating pair formation (Balakrishnan, 2016). Many insects produce long-distance 'calling' songs to attract and advertise to potential mates of the same species (Balakrishnan, 2016; Greenfield, 2002). However, such 'calling' songs are probably not applicable to bark beetles in the same sense, where acoustic signals are typically produced by the arriving sex as they approach the gallery entrance of the colonizing sex (Fleming et al., 2013; Kerchev, 2019; Lindeman & Yack, 2015). On the other hand, acoustic signals are proposed to function in conjunction with chemical and tactile communication in reproductive isolation, to prevent cross-breeding between closely related species (Kerchev, 2020; Oester & Rudinsky, 1978; Pureswaran et al., 2016; Ryker & Rudinsky, 1976a). If acoustic signals function in species recognition, it is predicted that in the initial stages of pair formation, there would be high stereotypy in at least one acoustic characteristic within a species, and little overlap between stereotyped characteristics in sympatric species (Balakrishnan, 2016; Greenfield, 2002). There is currently limited support for the role of acoustics in species isolation. Oester and Rudinsky (1978) show interspecies differences in

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premating chirps of three sympatric *Ips* species and suggest that sounds play a role in preventing hybridization. Yandell (1984) showed that male 'attractant' chirps in *D. ponderosae* were highly stereotyped in several acoustic features across different populations, supporting the species recognition hypothesis. Further investigations of interspecific and intraspecific variations of premating signals in sympatric species may help to uncover the role of acoustic communication in reproductive isolation in bark beetles.

Sexual selection

Acoustic signalling in insects can occur in contexts of intersexual selection (i.e. mate choice), where one sex chooses the opposite sex and intrasexual selection (i.e. competition), where there is rivalry between individuals of the same sex to compete for the opposite sex. Acoustic signalling in these non-mutually exclusive contexts commonly occurs in insects at close range and as components of courtship or rivalry displays (Alexander, 1961; Balakrishnan, 2016; Greenfield, 2002).

Intersexual selection

Acoustic courtship signals can play important roles in insect mating decisions by providing information about a potential mate's ability to contribute indirect benefits (genetic condition, survival ability) or direct benefits (e.g. parental care, food, territory defence) (Balakrishnan, 2016). Acoustic signals functioning in mate choice are typically produced at close range and vary between individuals in features that are indicative of mate quality. Signals conveying information about skill, power or body size, for example, may be longer, louder, more complex and repeated at a higher rate (Byers et al., 2010; Greenfield, 2002). Potential mates should show variability between individuals in these acoustic traits (Balakrishnan, 2016; Greenfield, 2002; Zuk et al., 2008). There is some evidence to support the hypothesis that acoustic signalling in bark beetles functions in mate choice decisions. First, in sound-producing species, once potential mates are attracted by long-distance aggregation pheromones, the attracted individuals often signal acoustically as they approach and try to gain access to the gallery entrance of the colonizing sex (Barr, 1969; Fleming et al., 2013; Kerchev, 2019). Second, potential mates that are silent (either naturally or by surgical manipulation) are either rejected completely or take longer to gain access to the gallery (Lindeman & Yack, 2015; Ryker & Rudinsky, 1976a). Third, signal traits of the arriving sex can vary between individuals and this variation has been correlated to mate choice decisions of the colonizing sex. For example, male *Dendroctonus* spp. (the arriving sex) produce two different types of chirps that have been categorized as simple and interrupted (Figures 4 and 5) (e.g. Fleming et al., 2013; Lindeman & Yack, 2015; Yturralde & Hofstetter, 2015). Lindeman and Yack (2015) demonstrated that in *D. valens*, females show a significant preference for males who produce more interrupted chirps than those who produce fewer or no interrupted chirps. This study proposed that interrupted chirps could be more energetically costly for males to perform, making them an honest indicator of a potential male's fitness. Sometimes the colonizing sex may produce sounds when the arriving sex is signalling, and different functions have been proposed for these signals (Fleming et al., 2013; Liu et al., 2017b; Ryker & Rudinsky, 1976b). Liu et al. (2017b) showed that males of *D. valens* used sounds to locate the female and discriminate body size. Acoustic 'dialogues' between potential mates are interesting and their functions require further study. In summary, while there is support for the hypothesis that acoustic signalling functions in mate choice, this requires further testing by assessing how acoustic traits are indicators of mate quality and how mate choices based on acoustic features result in increased fitness.

Intrasexual competition

In many insect species, same-sex competition for access to mates is a prevalent and critical aspect of mating dynamics (Miller & Svensson, 2014). Rivalry between same-sex individuals who endeavour to secure mating opportunities with potential partners may involve aggressive encounters, including wrestling, pushing or territorial disputes (Miller & Svensson, 2014). Acoustic rivalry signalling may play a role in competing for new resources, defending established resources (i.e. territoriality) or competing to attract the opposite sex. Predictions that support the hypothesis that acoustic signalling functions in intrasexual selection include the following: (1) if two individuals interact when one holds a resource, acoustic signalling will occur; (2) sometimes exchanges result in physical aggression and takeover by the rival and (3) acoustic features, such as signal rates, duration and loudness, are good predictors of who will win the contest (Balakrishnan, 2016; Greenfield, 2002). There is evidence for intrasexual selection in Scolytinae, as same-sex competition can occur in the initial stages of colonization, typically when a pioneering member begins tunnelling or shortly after pair formation (Kirkendall, 1983). Evidence for acoustically mediated intraspecific competition comes from rivalry studies between territory holders and intruders where the territory includes access to a mate (Kerchev, 2019; Liu et al., 2020; Oester et al., 1981; Rudinsky & Michael, 1974; Vernoff & Rudinsky, 1980). For example, studies on *Dendroctonus* spp. have reported that when an intruder male attempts to gain access to a female gallery already occupied by a resident male, either the resident male or both emit strong and continuous rivalry chirps accompanied by physical combat until the intruder male leaves the gallery (e.g. Liu et al., 2020; McGhehey, 1968; Rudinsky & Michael, 1974; Rudinsky & Ryker, 1976; Ryker & Rudinsky, 1976b).

Other functions

The functions of acoustic sensing and communication are likely to extend beyond the broad contexts of antipredator and reproductive contexts, given the incredible diversity in life history traits and social systems in Scolytinae (Kirkendall, 1983; Kirkendall et al., 2015; Raffa et al., 2015). Acoustic sensing and communication could be associated with various social interactions, host location, parental care, orientation, gallery construction and spacing, among other things. Here, we focus on two functions that have received some support: host location and spacing.

Many bark beetle species have been proposed to colonize drought-stressed trees that produce acoustic emissions with frequencies ranging from 80 to 2000 kHz in response to water stress (Haack et al., 1988; Mattson & Haack, 1987). To test if bark beetles are attracted to such sounds, preliminary laboratory tests were conducted using the mountain pine beetle, *D. ponderosae* (Kaiser, 2014). In these experiments, females, the primary colonizing sex in this species, were given a choice between a pine log with continuous playback of lodgepole pine acoustic emissions and those with no sound. Although the results were not statistically significant, there was a tendency to choose logs treated with acoustic emissions. The possibility that beetles can 'hear' stressed trees is an intriguing hypothesis that deserves further scrutiny.

Some bark beetles have the potential to become overcrowded, and avoiding competition for resources through spacing can be achieved at different stages of the life cycle, from deterring competitors to arrive at the same host plant to spacing between galleries inside the plant. Acoustic communication and sensing may play a role at different stages. In some *Dendroctonus* species, the gallery initiating sex (female) responds to the male's premating chirps by releasing anti-aggregation pheromones, an action that results in halting recruitment to the host tree to reduce competition (Rudinsky, 1969). Additionally, sound production may function as a means of spacing between members of the colonizing sex by claiming territories or boundaries. Acoustically mediated spacing has been suggested to operate at both larval and adult stages in bark beetles (see discussion of the role of acoustics in larval spacing in the Juveniles section). In adults, for instance, it is proposed that *Dendroctonus* spp. females use acoustic signals to mediate spacing while initiating a gallery on the bark surface (Rudinsky & Michael, 1973) and to prevent overlap of galleries in the phloem layer (Grosman et al., 1992).

SENSORY ORGANS AND SIGNAL TRANSMISSION

While acoustic communication is considered to be widely prevalent among bark beetles, neither sound nor vibration receptors have been identified. Confirmation of acoustic receptors in insects is based on morphological identification of sensory receptors, as well as neurophysiological and behavioural responses to biologically relevant sounds or vibrations (Yack & Fullard, 1993). Here we review the primary sensory mechanisms used by insects to detect far-field sounds, near-field sounds and solid-borne vibrations and then consider the likelihood of each of these occurring in bark beetles.

Far-field sounds refer to pressure waves that can be detectable at long distances from the source (up to a kilometre or more) (Strauß & Stumpner, 2015; Windmill & Jackson, 2016). Tympanal ears are used to detect far-field sounds and these types of ears in insects have evolved numerous times on many different body parts (Yack, 2004; Yager, 1999). They are often morphologically conspicuous, having a distinct membrane backed by a tracheal air sac (Yack, 2004; Yager, 1999). Near-field sounds refer to the displacement of air molecules close to the sound source and usually are low frequency (less than 1 kHz; Albert & Kozlov, 2016; Windmill & Jackson, 2016). Insects use lightweight sensory receptors such as setae or antennae to detect near-field sounds (Yack, 2004; Yack et al., 2020). Vibrations that travel through solids, such as plant materials, silk, wax and soil, are widely used by insects (Hill, 2008; Turchen et al., 2022; Yack, 2016). Subgenual organs, located in the leg tibia, are the most common type of vibration receptor in insects, although thought to be lacking in Coleoptera (Field & Matheson, 1998). Femoral chordotonal organs have been confirmed to detect vibrations in Coleoptera (Takanashi et al., 2016). Johnston's organs in antennae that are in contact with a substrate can also function as vibration receptors in insects (Jeram & Pabst, 1996).

Bark beetles have been proposed to receive far-field sounds in two general contexts: hearing the acoustic emissions of stressed trees and conspecific communication. While the possibility that beetles can detect ultrasonic emissions from cavitation events in water-stressed trees is an attractive hypothesis, there is limited support for this at the moment (see Functions of Acoustic Communication and Sensing section). In the context of conspecific communication, there are two lines of evidence for far-field hearing. First, sounds are potentially available, as they have been recorded using pressure-sensitive microphones at biologically relevant distances while bark beetles were interacting in a natural context (Dobai et al., 2018; Fleming et al., 2013; Lindeman & Yack, 2015). Second, sound playbacks have evoked behavioural responses in different contexts (Liu et al., 2020; Liu et al., 2017b). Currently, there is no morphological or neurophysiological evidence for tympanal ears in bark beetles; although, potential ears have been proposed for various body locations (Fleming, 2009; Hofstetter et al., 2019; Sivalinghem, 2011).

An alternative hypothesis is that bark beetles detect near-field sounds. Given the close distances between signalling beetles in natural contexts (usually within a few centimeters), this is a possibility. However, a couple of arguments challenge this hypothesis. First, the sounds produced by bark beetles tend to have dominant frequencies higher than 1 kHz (Bedoya et al., 2021), which is higher than those typically used by insects for near-field communication. Second, there is no documented evidence for potential near-field sound receptors, such as long lightweight setae or lightweight antennae. Despite these considerations, the possibility of bark beetles using near-field sound communication would be interesting to assess by measuring near-field sounds in natural contexts, especially within galleries.

Communication using solid-borne vibrations has also been proposed for bark beetles (Hofstetter et al., 2019) and this is an attractive hypothesis given that most social interactions occur on the bark surface or inside galleries. There is evidence that vibrations are available to beetles when interacting. For example, vibrations resulting from *I. pini* and *D. ponderosae* premating signals were recorded at biologically relevant distances using a laser vibrometer (Fleming et al., 2013; Sivalinghem, 2011). In another study, Bedoya et al. (2022) assessed the transmission of stress sounds emitted by *Hylastes ater* Erichson, 1836 and *Hylurgus ligniperda* (Fabricius, 1787) through bark and phloem tissues by recording vibrations with an accelerometer. Their findings revealed that signals were transmitted through phloem at behaviourally relevant distances, with many signal traits (spectral, temporal and amplitude) preserved up to several centimetres from the source. However, to date, there is little evidence for behavioural responses to vibroacoustic playback in bark beetles (Lukic et al., 2021).

JUVENILES

According to our literature review, only 2 out of 117 papers have proposed acoustic communication in bark beetle juveniles (including eggs, larvae and pupae). Bark beetle larvae in particular might be likely candidates for vibratory communication, as they can exhibit a number of social behaviours, including aggregation, as well as cooperation in spacing, feeding and gallery hygiene (Kirkendall et al., 2015). Indeed, vibratory communication is increasingly being acknowledged as an important means of communication in juvenile insects (Turchen et al., 2022; Yack, 2022; Yack & Yadav, 2022). The one example that has been discussed to date for bark beetles relates to larval gallery spacing.

In many phloeophagous species, eggs are laid in individual egg niches on either side of the parental gallery, and larvae radiate away from the parental gallery as they feed (Kirkendall et al., 2015; Wood, 2007) (Figure 1f). In some species, there is clear avoidance between larval galleries between siblings or neighbouring galleries of the same or other species (Byers, 1989; Trägårdh, 1930). Bark beetle larvae are proposed to space themselves to reduce food competition and avoid cannibalism (Trägårdh, 1930). Acoustic signals and cues have been proposed for larval spacing behaviour (Hofstetter et al., 2019). One key piece of evidence required to support the hypothesis is that larvae would be capable of producing acoustic signals or cues. Sounds and vibrations produced by movements and feeding are likely produced by Scolytinae larvae, as reported for other wood-boring larvae (Zorović & Čokl, 2015), but there is limited evidence supporting this at present. Matheson (2010) recorded larvae of *Scolytus multistriatus* (Marsham, 1802) in a phloem sandwich using a laser vibrometer and confirmed that short-duration vibrations coincided with feeding behaviour. Other potential evidence of vibratory-mediated spacing in Scolytinae larvae derives from a modelling study. Modelling was employed to assess how *Ips typographus* (Linnaeus, 1758) and *Tomicus piniperda* (Linnaeus, 1758) larvae could avoid competition for food resources and space within confined feeding galleries. The models predicted that larvae possess the ability to detect ‘sounds’ within an 8 mm radius for *T. piniperda* and a 10 mm radius for *I. typographus*, effectively preventing interference with their siblings. The authors proposed that the ability to recognize and respond to other larvae in close proximity may confer notable advantages for survival (De Jong & Grijpma, 1986; De Jong & Saarenmaa, 1985). Future research could employ vibratory recordings conducted in combination with video recordings, as well as vibration playbacks, to test if larvae produce and/or respond to vibrations.

PRACTICAL APPLICATIONS FOR BARK BEETLE ACOUSTICS

Acoustic technologies are increasingly being tested and employed as viable options to manage insect pests (Bhairavi et al., 2020; Mankin et al., 2011; Polajnar et al., 2015) and are considered to be promising for bark beetles (Hofstetter et al., 2019). Here we discuss how acoustic technologies might best be employed to identify, monitor, trap or manipulate the behaviour of bark beetles.

Acoustic monitoring of insects has been used to identify species and estimate population densities for early detection of pests (Mankin et al., 2011, 2021). This technology has potential for bark beetles given the wide variation in acoustic signals (Barr, 1969; Bedoya et al., 2021; Hofstetter et al., 2019), in addition to incidental sounds and vibrations resulting from chewing or movement within the galleries (Allen et al., 1958; Matheson, 2010; Rochester, 2020). To develop automatic recognition systems, it is necessary to build a database of sounds and vibrations recorded for species of interest in different behavioural contexts, to characterize these signals and identify distinguishing species-specific features, and finally, to test the efficacy of the proposed application. In a pilot study, Lindeman (2015) tested an acoustic identification system by recording and characterizing sounds of three sympatric species—*D. ponderosae*, *D. valens* and *I. pini*. Distinguishing features between the species were based on temporal and amplitude envelope features. Machine learning classifiers (i.e. random forests and support vector machines) were used to distinguish between species that exhibited approximately 60% accuracy. In another study, Bedoya et al. (2022) used two bark beetle species, *H. ater* and *H. ligniperda*, to develop and test algorithms for an automatic identification system. Acoustic signals were recorded using an accelerometer when beetles were placed in pre-drilled holes at different distances from the recording device. Using five acoustic spectro-temporal characteristics, the two species could be identified with a 99% accuracy when the beetle is within 20 cm of the recording device.

Sounds or vibrations have been used to trap insect pests that exhibit phonotactic behaviours (Mankin, 2012). To date, there is little support for positive phonotactic behaviours in bark beetles (but see Liu et al., 2020). However, there are a couple of contexts to explore. The first is the possibility that beetles are attracted to acoustic emissions of stressed trees to locate potential hosts, and the second is the potential orientation towards alarm calls from conspecifics (see discussion in the Functions of Acoustic Communication and Sensing section of this paper).

Sound and vibration playbacks have been used to manipulate insect behaviour in the context of integrated pest management (Mankin et al., 2011; Polajnar et al., 2015). In bark beetles, acoustic playbacks have been tested for manipulation of host selection, gallery formation and reproductive behaviours. Aflitto and Hofstetter (2014) investigated the impact of playbacks on host selection in three species, *D. brevicomis*, *D. frontalis* and *I. pini*. Beetles were offered a choice between a log with no 'sound' and a log with various 'sounds', including species-specific signals, a computer-generated tone and a wood borer (*Monochamus titillator* (Fabricius, 1775)) stress signal, delivered by a tactile transducer attached to the xylem. Some acoustic treatments moderately influenced log entry rates in the two *Dendroctonus* species, but not in *I. pini*. Another potential method to impede host selection would be to treat host trees with male *Dendroctonus* sounds, shown to stimulate the release of anti-aggregation pheromones (Liu et al., 2017a; Rudinsky et al., 1973). This may have the potential to impede mass attacks but requires testing in the field. Hofstetter et al. (2014) investigated the impacts of various sound playbacks, including modified beetle signals and anthropogenic sounds, on the reproductive behaviour and survival of adult *D. frontalis* in phloem sandwiches. Playbacks resulted in reduced lengths of the excavated tunnels and fewer deposited eggs. While playback studies show potential in manipulating the behaviour of bark beetles, there are certain challenges with respect to implementing these methods in the field (Hofstetter et al., 2019).

SUMMARY AND CONCLUSIONS

Acoustic communication in bark beetles is taxonomically widespread and diverse with respect to mechanisms of sound production and functions, but there is much to learn about this fascinating system. We identify gaps in our knowledge and make recommendations to guide further research.

Diversity and evolution

While the subfamily Scolytinae has more than 6000 described species, only about 3% have been examined in the context of sound production. Many species have never been examined morphologically for stridulatory organs and far fewer have been tested for sound production. We recommend that species from under-represented tribes (see Figure 3b; Table S1) be examined for sound production capabilities. It is recommended that both sexes be examined for morphological evidence of stridulatory organs and also tested for sound production in different behavioural contexts. When conducting acoustic recordings, attempts should be made to record both sounds and vibrations under natural conditions and using instrumentation that will allow for full characterization of signals (e.g. broadband microphones, recordings with high sampling rates). These data on taxonomic diversity can be used to test hypotheses on the functions and evolution of acoustic communication using comparative phylogenetics.

Functions of acoustic communication in adults

Despite numerous reports of bark beetles producing acoustic signals in different contexts, our understanding of the adaptive value of these signals remains limited. Most studies have recorded airborne sounds from one or two individuals in either an artificial context (e.g. pinching by humans, forced interactions in a dish) or on the log surface at the gallery entrance. However, little is known about acoustic communication inside the galleries where many interactions occur between adults, larvae and other organisms. Developing methods to simultaneously record acoustic signals and behaviours in natural contexts, for example by using phloem sandwiches, laser vibrometry, as well as probe microphones and cameras, will shed light on the complexity of communication dynamics. Also, comparative phylogenetics could be explored to test hypotheses on the functions of acoustic behaviour.

How do bark beetles sense acoustic signals?

Acoustic sensory organs have not yet been identified for any species of bark beetles. Also, it is uncertain whether acoustic signals are received through air (as sounds) or solids (as vibrations) or both. Future research should focus on conducting the following types of experiments: (1) neurophysiological recordings on peripheral nerves, connectives or the central nervous system, combined with morphological studies to identify possible sensory organs; (2) sound and vibration recordings under natural conditions to assess how signals are transmitted at biologically relevant distances and (3) sound and vibration playbacks to assess behavioural responses to signals.

Do juveniles use acoustic signals or cues?

There is increasing evidence that larval insects use vibrations to communicate (Turchen et al., 2022) and it has been hypothesized that bark beetle larvae use vibrations to space themselves between feeding galleries. Also, as bark beetle larvae are reported to interact socially among themselves and with adults, the possibility of such interactions being acoustically mediated could be explored by recording acoustic events in natural or semi-natural environments and by conducting playback experiments.

Practical applications

Many species of bark beetles are devastative forest pests and there is interest in using acoustic technologies as environmentally friendly approaches to monitor and control these pests. Based on our understanding of the acoustic sensory ecology of bark beetles to date, the most promising applications are the following: (1) species identification and monitoring based on species-specific signal features of adults; (2) behavioural manipulation through vibroacoustic playbacks.

AUTHOR CONTRIBUTIONS

Elham Arjomandi: Conceptualization; data curation; investigation; methodology; project administration; validation; visualization; writing – review and editing; writing – original draft. **Leonardo**

M. Turchen: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Amanda A. Connolly:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing; writing – original draft. **Michelle B. Léveillée:** Data curation; investigation; methodology; writing – review and editing. **Jayne E. Yack:** Data curation; investigation; methodology; writing – review and editing; conceptualization; project administration; resources; supervision; validation; visualization; funding acquisition; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ETHICS STATEMENT

This article does not contain any studies with human participants or animals.

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SUPPORTING INFORMATION

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

Table S1. List of tribes and species of bark beetles[1] (Curculionidae: Scolytinae) that are reported to use acoustic sensing or communication based on morphology, sound recordings, or behaviour. Sex examined: The sex examined for any evidence of acoustic sensing or communication, ♂: male, ♀: female, NA: sex was not indicated. Stridulatory Organ: Type of stridulatory organ including E-T: Elytro-tergal, V-Pr: Vertex-pronotal, G-Pr: Gula-prosternal, P-S: Pygidium-sternal, E-Ti: Elytro-tibial; NA was used when no stridulatory organ was reported. Context: Behavioural contexts under which examined beetles are reported to produce or detect sounds or vibrations. The term Distress may include contexts where individuals were stimulated by probing, pinching or stroking. Sound recorded: Species that were tested for sound production (Y: Yes or N: No). Sex reported to produce sound: Evidence for sound production reported.

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