LEONARDO MORAIS TURCHEN

VIBROACOUSTICS OF INSECTS: A META-ANALYSIS AND THE FIRST EXPEDITION INTO THE HITHERTO UNKNOWN VIBRATORY WORLD OF THE FALL ARMYWORM

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para a obtenção do título de *Doctor Scientiae*.

Orientador: Raul Narciso Carvalho Guedes

Coorientador: Jayne Elizabeth Yack

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Orientador

I dedicate this thesis to my mother Ana Claudia Lemes de Morais and my sister Paloma Morais Turchen, for their endless love, support, and encouragement

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ABSTRACT

TURCHEN, Leonardo Morais, D.Sc., Universidade Federal de Viçosa, November, 2021**.** **Vibroacoustics of insects: a meta-analysis and the first expedition into the hitherto unknown vibratory world of the fall armyworm.** Advisor: Raul Narciso Carvalho Guedes. Co-advisor: Jayne Elizabeth Yack.

Vibratory sensing and communication in insects has been researched for decades, and this sensory modality has recently garnered popularity in the scientific community. There is an increasing body of evidence demonstrating (or suggesting) the relevance of solid-borne vibrations in a wide range of insect behaviors, from passive cue detection to complex communication signals. Despite growing awareness of this sensory modality, many questions remain unanswered. My Ph.D. dissertation was divided into two chapters to address some of these issues. First, a systematic survey with meta-analyses was performed to identify knowledge gaps and biases in these research topics. The survey tracked 831 papers during the last 75 years, which exhibited exponential growth since the 1990s, and reported 17 insect orders associated with vibratory events. In these studies, three prominent biases were detected: i) prevalence of studies on Hemiptera, Hymenoptera, and Coleoptera; and ii) a focus on adults, with far less attention to juveniles; and iii) on reproductive behaviors, with less attention to other behavioral contexts. Other gaps were identified, such as a lack of study on most insects' vibration landscapes and a lack of research on the processes employed by insects to perceive and process vibrations, both of which require more investigation. In the second chapter, an experiment was conducted to characterize relevant vibrations in the landscape of a caterpillar using spatial analysis, and, subsequently, to test whether fall armyworm larvae can detect and respond to vibrations from the wind, raindrops, conspecifics, and heterospecifics (a predatory stinkbug). The results show that vibrations from abiotic and biotic stimuli were distinct from background noise, except those produced by the crawling of 1st instar larvae. Moreover, the spatial analysis revealed that vibrations exhibit contrasting distribution patterns in the leaf depending on their origin. Vibrations caused by simulated wind and raindrops were more widely spread across the leaves. In contrast, the vibrations produced by fall armyworm crawling or stinkbug walking were concentrated on some leaf regions. Our findings also supported the hypothesis that fall armyworm larvae are able to detect abiotic and biotic vibrations and respond to them. Caterpillars exposed to wind and rain stimuli behaved differently than unexposed caterpillars, regardless of instar. Caterpillars exposed to wind responded with a greater transition from crawling to touching around, whereas caterpillars exposed to raindrops responded with a greater transition from crawling to resting. Caterpillars exposed to biotic stimuli did not exhibit a consistent response among instars, as first instars did not respond to the approach of a conspecific or a predator, whereas caterpillars from second to fifth instars responded. When approached by a conspecific, caterpillars spend less time feeding and more time crawling, touching around, or resting, and eventually produce defensive behaviors. In contrast, caterpillars exposed to predators spend more time freezing, feeding, and resting, eventually exhibiting other defensive behaviors. In conclusion, these findings shed new light on the vibroacoustic landscapes of insects. First, they identify major gaps in the literature, indicating that future studies should focus on a larger variety of orders and higher taxa (i.e., genera, families, and species), including the significance of vibration in various adaptive contexts and how both adults and juveniles (i.e., eggs, larvae/nymphs, and pupae) use vibrations. These findings also provide new insights into a caterpillar's vibratory landscape on a leaf scale utilizing spatial analysis, revealing that complex vibratory environments exist even on a small scale. It also supports the hypothesis that fall armyworm larvae can detect and respond to both abiotic and biotic vibrations in order to survive.

Keywords: Behavior. Biotremology. Caterpillar. Insects. Predatory stinkbug. Solid-borne vibrations. Spatial distribution. Vibrational communication.

RESUMO

TURCHEN, Leonardo Morais, D.Sc., Universidade Federal de Viçosa, novembro de 2021. **Vibroacustica de insetos: uma meta-análise e a primeira expedição ao até então desconhecido mundo vibratório da lagarta-do-cartucho.** Orientador: Raul Narciso Carvalho Guedes. Coorientadora: Jayne Elizabeth Yack.

A detecção vibratória e a comunicação em insetos têm sido pesquisadas há décadas, e recentemente essa modalidade sensorial ganhou popularidade na comunidade científica. Há um crescente corpo de evidências demonstrando (ou sugerindo) a relevância das vibrações de origem sólida em uma ampla gama de comportamentos de insetos, desde a detecção de sinal passivo até sinais de comunicação complexos. Contudo, apesar da crescente conscientização desta modalidade sensorial, muitas perguntas ainda permanecem sem resposta. A minha tese de doutorado foi dividida em dois capítulos para abordar algumas dessas questões. No primeiro, uma pesquisa sistemática com meta-análises foi realizada para identificar lacunas e vieses de conhecimento neste tópico de pesquisa. A pesquisa rastreou 831 artigos durante os últimos 75 anos, os quais exibiram um crescimento exponencial desde a década de 1990 e reportaram 17 ordens de insetos associados a eventos vibratórios. Nestes estudos, três vieses proeminentes foram detectados: i) a prevalência de estudos em Hemiptera, Hymenoptera e Coleoptera; ii) o foco nos adultos, com menor atenção aos juvenis; e iii) a prevalência de estudos em comportamentos reprodutivos, com menor atenção a outros contextos comportamentais. Outras lacunas também foram observadas, como a falta de pesquisas sobre a paisagem vibratória da maioria dos insetos, bem como a carência de pesquisas sobre os mecanismos usados por insetos para perceber e processar as vibrações, ambos os quais precisam de mais investigações. No segundo capítulo, foi realizado um experimento para caracterizar vibrações relevantes na paisagem de uma lagarta por meio de análise espacial e, em seguida, testar se as larvas da lagarta-do-cartucho podem detectar e responder a vibrações oriundas de vento, gotas de chuva, coespecífico e heteroespecífico (no caso, percevejo predador). As vibrações dos estímulos abióticos e bióticos foram distintas do ruído de fundo, exceto aqueles produzidos pelo caminhamento de larvas de primeiro instar. Além disso, a análise espacial apontou que dependendo da origem as vibrações exibem padrões de distribuição contrastantes na folha. Vibrações produzidas por vento e gotas de chuva simulados espalhou-se mais amplamente pelas folhas. Em contraste, as vibrações produzidas pela caminhada da lagarta-do-cartucho ou do percevejo, concentraram-se em algumas regiões das folhas. Nossos resultados também suportam a hipótese de que as larvas da lagarta-do-cartucho são capazes de detectar e distinguir vibrações abióticas e bióticas e responder a elas. As lagartas expostas aos estímulos do vento e da chuva se comportaram de maneira diferente das não expostas, independentemente do instar. Lagartas expostas ao vento responderam com uma transição maior de rastejar para tocar ao redor, enquanto as lagartas expostas a gotas de chuva responderam com uma transição maior de rastejar para descansar. Por outro lado, lagartas expostas a estímulos bióticos não exibiram uma resposta consistente entre os ínstares, uma vez que o primeiro ínstar não respondeu à abordagem de um coespecífico ou predador, enquanto as lagartas do segundo ao quinto ínstares responderam. Quando abordadas por um coespecífico, as lagartas passaram menos tempo se alimentando e mais tempo rastejando, tocando ou descansando e, eventualmente, exibiram comportamentos defensivos. Em contraste, as lagartas expostas a predadores passam mais tempo imóveis, se alimentando e descansando e, eventualmente exibiram comportamentos defensivos. Em conclusão, esses achados lançam uma nova luz sobre a vibroacústica de insetos. Primeiro, eles identificam as principais lacunas na literatura, indicando que estudos futuros devem se concentrar em uma variedade maior de ordens e taxons superiores (ou seja, gêneros, famílias e espécies), incluindo a importância da vibração em vários contextos adaptativos e como os adultos e os juvenis (ou seja, ovos, larvas / ninfas e pupas) usam vibrações. Essas descobertas também fornecem novos perspectivas sobre a paisagem vibratória de uma lagarta em uma escala de folha utilizando a análise espacial, revelando que ambientes vibratórios complexos existem mesmo em uma pequena escala. Também apoia a hipótese de que larvas de lagarta do cartucho detectam e respondem a vibrações abióticas e bióticas para sobreviver.

Palavras-chave: Comportamento. Biotremologia. Lagarta. Insetos. Percevejo predador. Vibrações em superfície sólidas. Distribuição espacial. Comunicação vibracional.

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GENERAL INTRODUCTION

The world around us is filled with sights, sounds, smells, and textures that activate our various sensory systems and enable us to properly interact with the environment (Stevens 2013). On a smaller scale, the world of insects is as fascinating, complex, and mysterious as it is on a human scale. This is because insects, too, have many sensory channels that extract information from the environment and convert it into adaptive behavioral responses (Yack 2004). However, they commonly do not perceive the world in the same way that humans do. The vibratory sense is an excellent illustration of this, as much of the vibrational information available in the environment is not available to humans (particularly infra and ultra-frequency vibrations) but are recognized and used by the majority of animals (Hill 2009), including insects (Cocroft & Rodríguez 2005; Yack 2016). In recognition of this observation, I chose to venture into the vibratory world of insects in my Ph.D., as it is fascinating to think that mechanical waves (vibrations) with frequencies imperceptible to our ears can play a critical role in the life history of insects and many other organisms, demonstrating that "*...some infinities are bigger than others...*", as predicted by Russia-born German mathematician Georg Cantor, which also drew my interest.

As a start, it is necessary to define the term "vibratory." This is crucial because acoustic signals and events are defined as vibrations transmitted through an elastic medium such as air, water, or solids. However, my research focused only on the vibration transmitted by solid surfaces. Therefore, when I say "vibration," I am referring to mechanical waves transmitted via solid substrates (e.g., soil, plant material, silk, wax), as opposed to those transmitted by fluids, such as air or water, and commonly referred to as "sounds" (see Hill 2008; Hill & Wessel, 2016). These vibrations are ubiquitous in the environment and originate from abiotic and biotic sources. Nonetheless, only in the last three decades have scientists begun to study and dedicate their attention to this phenomenon (Hill 2008; Cocroft et al. 2014; Hill & Wessel 2016; Hill et al. 2019). As a result, there is a growing body of evidence demonstrating the importance of solid-borne vibrations in a variety of insect behaviors, ranging from passive cue detection to complex communication signals (Virant-Doberlet & Čokl 2004; Cocroft & Rodríguez 2005; Cocroft et al. 2014; Hill et al. 2019). Despite growing awareness of the vibratory sensory modality in insects, many questions remain unanswered about which taxa use vibrations, how they use them, the characteristics and transmission properties of signals and cues in natural habitats, and the sensory mechanisms used to detect and process vibratory stimuli.

In this research, the fall armyworm, *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera: Noctuidae) was used as an experimental model for a first expedition into the vibrating world of insects. Lepidoptera are insects that exploit most terrestrial ecosystems and integrate the ecological web, where they participate in numerous processes, including pollination (James et al. 2018). However, this order is primarily known for its economic importance, as lepidopteran larvae are phytophagous and often make up the complex of cultivated (i.e., agricultural and forestry) plant pests. Caterpillars—the immature stage of moths and butterflies—are obligate substrate-bound and exhibit a curious life history. From when they hatch from eggs and begin their search for food, they face the daunting task of coping with a complex environment that includes biotic and abiotic noise. Furthermore, the caterpillars are prey and hosts of a variety of predators and parasitoids. Consequently, it is presumed that they have evolved a range of survival techniques that have helped make the Lepidoptera one of the most successful insect orders. Within this context, it seems likely that the ability to detect and distinguish plant-borne vibrations plays a prominent role in the sensory ecology and survival of caterpillars (Yack 2016). In the literature, there is a growing number of papers demonstrating or suggesting that caterpillars are capable of detecting and discriminating between vibration sources in a variety of contexts, including predator detection and risk assessment (Castellanos & Barbosa 2006), detection of abiotic events such as wind and rain (Guedes et al. 2012), recruitment and spacing (Fletcher et al. 2006; Yadav et al. 2017), territorial defense (Yack et al. 2001; 2014), and maintaining relationships with ants (Travassos & Pierce 2000; Casacci et al. 2019). Even so, the natural vibratory landscapes of caterpillars living on different plant substrates, and who are exposed to a range of different biotic and abiotic factors, remain poorly understood for most species.

This dissertation has been organized into two chapters to explore some of these gaps. In the first chapter, the objective was to perform a systematic literature review and meta-analysis over a period of 75 years to obtain an overview of the strengths and weaknesses of the field, as well as to summarize the temporal trends and test the biases regarding taxa, developmental stages, and research topics reported in scientific papers. In the second chapter, the objective was to record and characterize the vibroacoustic landscape on a leaf scale in the presence of abiotic (wind and raindrops) and biotic stimuli (caterpillars and predatory stinkbug) using a laser-doppler vibrometer, and also test whether the different instars of the fall armyworm detect and respond to those vibrations.

REFERENCES

Casacci, L. P., Bonelli, S., Balletto, E., & Barbero, F. (2019). Multimodal signaling in myrmecophilous butterflies. *Frontiers in Ecology and Evolution*, 7, 454. https://doi.org/10.3389/fevo.2019.00454

Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, 72, 461-469. https://doi.org/10.1016/j.anbehav.2006.02.005

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, 55, 323-334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO,2

Cocroft, R. B., Gogala, M., Hill, P. S. M., & Wessel, A. (2014). *Studying vibrational communication*, Springer. https://doi.org/10.1007/978-3-662-43607-3

Fletcher, L. E., Yack, J. E., Fitzgerald, T. D., & Hoy, R. R. (2006). Vibrational communication in the cherry leaf roller caterpillar *Caloptilia serotinella* (Gracillarioidea: Gracillariidae). *Journal of Insect Behavior*, 19, 1-18. https://doi.org/10.1007/s10905-005-9007-y

Hill, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften*, 96, 1355-1371. https://doi.org/10.1007/s00114-009-0588-8

Hill, P. S., & Wessel, A. (2016). Biotremology. *Current Biology*, 26, R187-R191. https://doi.org/10.1016/J.CUB.2016.01.054

Hill, P.S.M. (2008). *Vibrational communication in animals*. Harvard University Press.

Hill, P.S.M., Lakes-Harlan, R., Mazzoni, V., Narins, P.M., Virant-Doberlet, M., & Wessel, A. (2019). *Biotremology: Studying vibrational behavior*, Springer. https://doi.org/10.1007/978-3-030-22293-2

James, D. G., Morgan, S., & Sourakov, A. (2018). *The book of caterpillars: a life-size guide to six hundred species from around the world*. University of Chicago Press.

Stevens, M. (2013). *Sensory ecology, behaviour, and evolution*. Oxford University Press.

Travassos, M. A., & Pierce, N. E. (2000). Acoustics, context and function of vibrational signalling in a butterfly-ant mutualism. *Animal Behaviour*, 60, 13–26. https://doi.org/10.1006/anbe.1999.1364

Virant-Doberlet, M., & Čokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33, 121-134. https://doi.org/10.1590/s1519-566x2004000200001

Yack, J. E., Smith, M. L., & Weatherhead, P. J. (2001). Caterpillar talk: acoustically mediated territoriality in larval Lepidoptera. *Proceedings of the National Academy of Sciences*, 98, 11371-11375. https://doi.org/10.1073/pnas.191378898

Yack, J. E. (2004). The structure and function of auditory chordotonal organs in insects. *Microscopy research and technique*, 63, 315-337. https://doi.org/10.1002/jemt.20051

Yack, J. E., Gill, S., Drummond-Main, C., & Sherratt, T. N. (2014). Residency duration and shelter quality influence vibratory signalling displays in a territorial caterpillar. *Ethology*, 120, 354-364. https://doi.org/10.1111/eth.12210

Yack, J. E. (2016). Vibrational signaling. In G. S. Pollack, A. C. Mason, A. N. Popper, R. R. Fay (Eds.), *Insect hearing* (pp. 99–123). Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-28890-1_5

Yadav, C., Guedes, R. N. C., Matheson, S. M., Timbers, T. A., & Yack, J. E. (2017). Invitation by vibration: recruitment to feeding shelters in social caterpillars. *Behavioral Ecology and Sociobiology*, 71, 51. https://doi.org/10.1007/s00265-017-2280-x

CHAPTER 1

Bug talk trends & biases: literature survey and meta-analyses of vibratory sensing and communication in insects

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Short title: Bug talk trends & biases: insect biotremology

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Abstract

Research on insect biotremology has resulted in a burgeoning body of literature over the past few decades. Despite this, several biases and knowledge gaps have been proposed, but not quantified. Therefore, a systematic literature review and meta-analyses was carried out to summarize the temporal trends and test for biases regarding taxa, developmental stages, and research topics reported in scientific papers spanning 75 years. The survey tracked 831 papers, which exhibited exponential growth since the 1990s and covered 17 insect orders. Among these studies, 70.4% were associated with adaptive behaviors, while the remaining (29.6%) focused on applied entomology and sensory organs. Three main biases were detected: (i) a prevalence of studies on Hemiptera, Hymenoptera, and Coleoptera, (ii) a focus on adults, and (iii) a preponderance of studies on reproductive behaviors. Considering only adaptive behaviors, the likelihood of studies with adults was 3x higher than for juveniles. Studies documenting receiver response were 2x higher than not. Still, few insect orders (9 of 17) included reports on vibrations used in an adaptive context, while studies reported in the remaining orders focusing on mechanisms of vibration production or vibration characteristics. The results of this study highlight knowledge gaps worthy of future investigations. In particular, further research is necessary on the role of vibratory sensing and communication in juveniles (eggs, larvae, pupae, and nymphs), testing hypotheses on the adaptive roles of vibrations in a broader range of taxa, characterization of vibratory landscapes, and research on sensory receptors.

Keywords: biotremology; development; substrate-borne vibrations; vibroacoustic; behavior; Insecta.

Introduction

Vibratory sensing and communication are considered to be one of the most ubiquitous and ancient sensory modalities in insects (Hill 2009; Endler 2014). By vibration, we refer to mechanical waves transmitted through solids (e.g., soil, plant material, silk, wax), in contrast to those transmitted through air or water and commonly referred to as “sounds” (see Hill 2008; Hill & Wessel 2016). Solid-borne vibrations are widely available to insects in the environment and originate from both abiotic (e.g., rain, wind) and biotic (e.g., conspecifics, predators) sources. Vibrations arising from biotic sources can be produced incidentally as cues, such as when an insect walks, or directly as signals, such as when an insect communicates to a mate (Maynard-Smith & Harper 2003; Yack 2016; Giunti et al. 2018). Vibratory sensing and communication (or biotremology, a recently coined term) in insects has received increasing research attention over the past few decades and this field of study has been variously described as a 'gold mine' with 'unsurpassed opportunities' (Cocroft et al. 2014a), and an 'unchartered territory' (Yack 2016), with 'many opportunities for ground-breaking study' (Cocroft & Rodríguez 2005). Despite the progress of this field, there are questions unanswered and gaps in our knowledge that deserve scrutiny.

A number of reviews have covered the topic of vibratory sensing and communication in insects to varying degrees. These include comprehensive reviews that focus on the distribution of taxa and contexts in general (e.g., Virant-Doberlet & Čokl 2004; Cocroft & Rodríguez 2005), or specific taxonomic groups (e.g., Plecoptera [Stewart 1997], Neuroptera [Devetak 1998; Henry et al. 2012; 2013], Hemiptera [Gogala et al. 1974; Claridge 1985; Čokl & Virant-Doberlet 2003; Cocroft & Mcnett 2006], Hymenoptera [Schneider & Lewis 2004; De-Luca & Vallejo-Marin 2013]; Mantophasmatodea [Eberhard & Eberhard 2013]). Others focus on the role of vibrations mediating specific types of interactions such as group-living (e.g., Cocroft 2001; Hunt & Richard 2013), prey-predator (e.g., Casas & Magal 2006; Virant-Doberlet et al. 2019), and myrmecophily (e.g., Casacci et al. 2019). Others address practical applications for insect monitoring and control (e.g., Rajendran 1999; Polajnar et al. 2015; Liu et al. 2017; Banga et al. 2018; Takanashi et al. 2019; Adedeji et al. 2020; Lima et al. 2020).

Based on the literature reviewed to date, a number of potential shortcomings and biases have been noted. The first relates to which insects detect and generate vibration. It has been stated that we are in the process of "identifying the players" including taxa never considered before (Hill 2008; 2009; Yack 2016). To the best of our knowledge, eighteen insect orders have been qualitatively recognized as using vibratory communication and sensing (Virant-Doberlet & Čokl 2004; Cocroft & Rodriguez 2005), but without a more in-deep analysis and quantitative assessment. However, this number has been estimated as being low, leaving out some of the small-bodied orders (e.g., fleas, twisted wing parasites, jumping bristletails, and thrips). Second, it is proposed that research has focused on adult insects (Virant-Doberlet & Čokl 2004; Cocroft et al. 2014b; Yack 2016), which is a conundrum because juveniles are generally more substrate-bound than their adult counterparts, given that they are less likely to jump and do not fly. Third, it has been proposed that topics covered are biased towards some subjects, such as reproduction (see Virant-Doberlet & Čokl 2004; Cocroft et al. 2014b; Hill et al. 2019), but lacking in others, such as sensory organs (Yack 2016) and evolution (Hill et al. 2019). Finally, while there are many reports of proposed vibration sensing and communication, for example, based on morphology alone or recorded vibrations (e.g., Low 2008; Quiroga et al. 2019), it is not always clear whether these examples constitute adaptive usage of vibrations, as experimental evidence for information transfer is lacking. The above-mentioned concerns led to the present attempt to understand how vibratory sensing and communication has been studied in insects.

The purpose of this review is to survey the literature over a period of 75 years, from 1945 to 2020, to obtain an overview of strengths and weaknesses in the field. This study had two primary goals. First, to conduct a systematic literature survey to qualitatively describe the temporal trends in publications, the taxonomic groups, and developmental stages, and to identify the main topics studied. This was done using the *Web of Science* and *Scopus* databases. The second goal was to conduct meta-analyses to synthesize, quantify and test the investigation trends, with the purpose of testing specifically: (i) whether there is a prevailing bias on the development stages studied, and (ii) whether there was evidence for receiving vibrations (cues or signal) in an adaptive context. Note that our intention was not to conduct a complete and global survey of all literature covering the topic of insect vibratory sensing and communication, but rather to carry out a comprehensive survey of a subset of the literature within our search constraints to identify trends. The results allow for the recognition of knowledge gaps and provide directions for further investigation.

Materials and methods

The procedures for the systematic literature survey and subsequent meta-analyses followed the guidelines of "*Preferred Reporting Items for Systematic Reviews and Meta-Analyses*" (PRISMA) (Moher et al. 2009), which are briefly described below.

Initial data collection, screening, and literature review

An overview of the process of data collection and screening is described in Fig. 1. First, a literature search was performed on the topic of vibratory sensing and communication among insects. We used combinations of keywords in two databases (*Web of Science* and *Scopus*), including literature published over a 75-year period, between January 1945 and December 2020. The search was carried out with general keywords to identify a broad initial dataset, and included the following terms: "bioacoustics," "acoustic," "vibratory," "vibration," "vibroacoustic," "substrate-borne," "solid-borne," "vibrational," "seismic," or "biotremology," in mandatory combination with "herbivore," "insect," "arthropod," "Insecta" or "phytophagous." Afterward, we included the references from the book by Cocroft et al. (2014b), which contains a comprehensive review on vibratory communication with an emphasis on arthropods. Duplicate papers were removed from the dataset, and the remaining were further screened for inclusion in the qualitative analysis by including in our dataset only studies that met the following criteria: (i) were published in English in a peer-reviewed journal; (ii) contained the target organism (i.e., insect) and solid-borne vibrations, and iii) reported the developmental stage of the organism studied (adults or juveniles). We excluded any narrative review, case report, protocol, editorial, book, book chapter, thesis, dissertation, and proceedings of meetings or conferences.

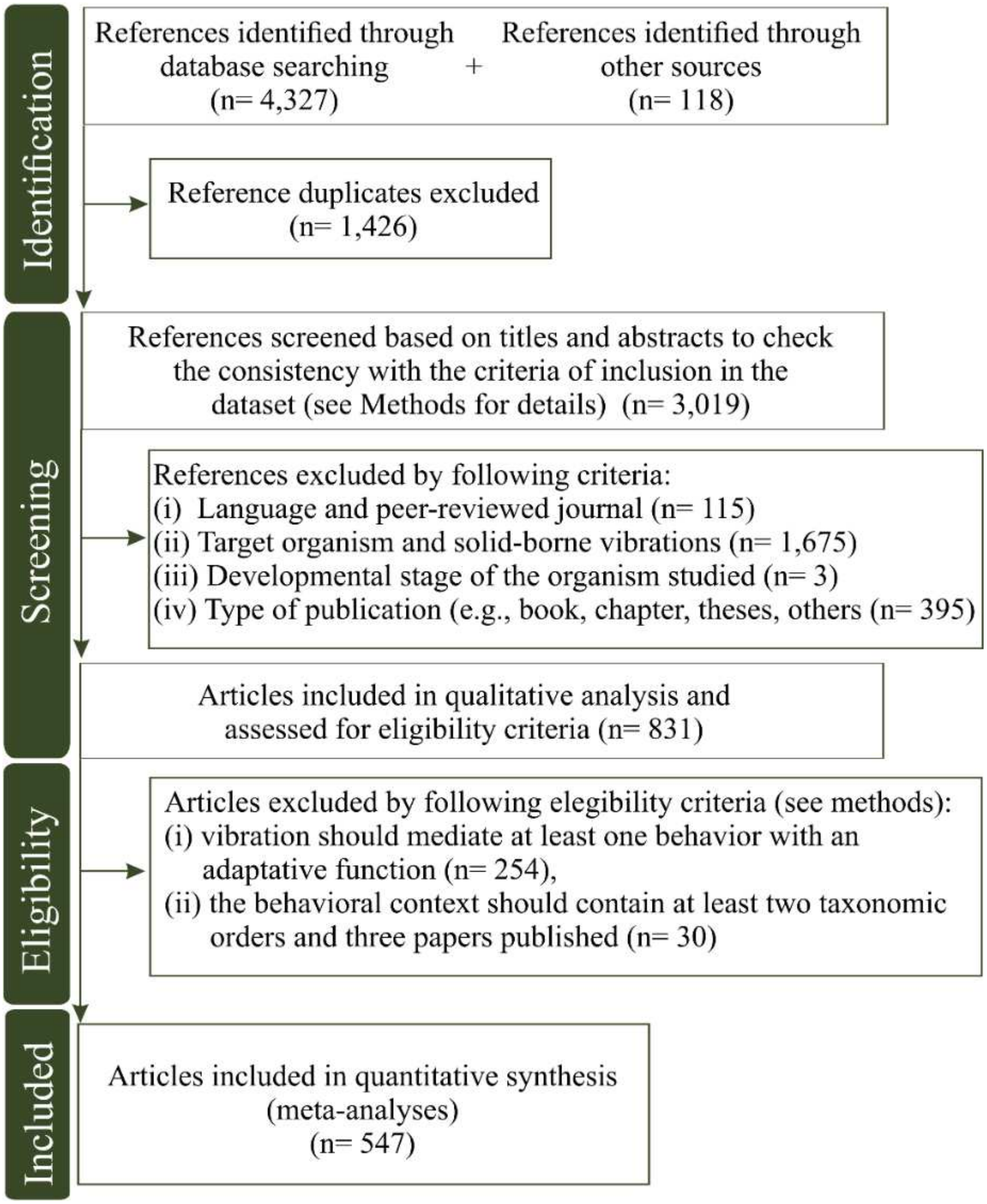
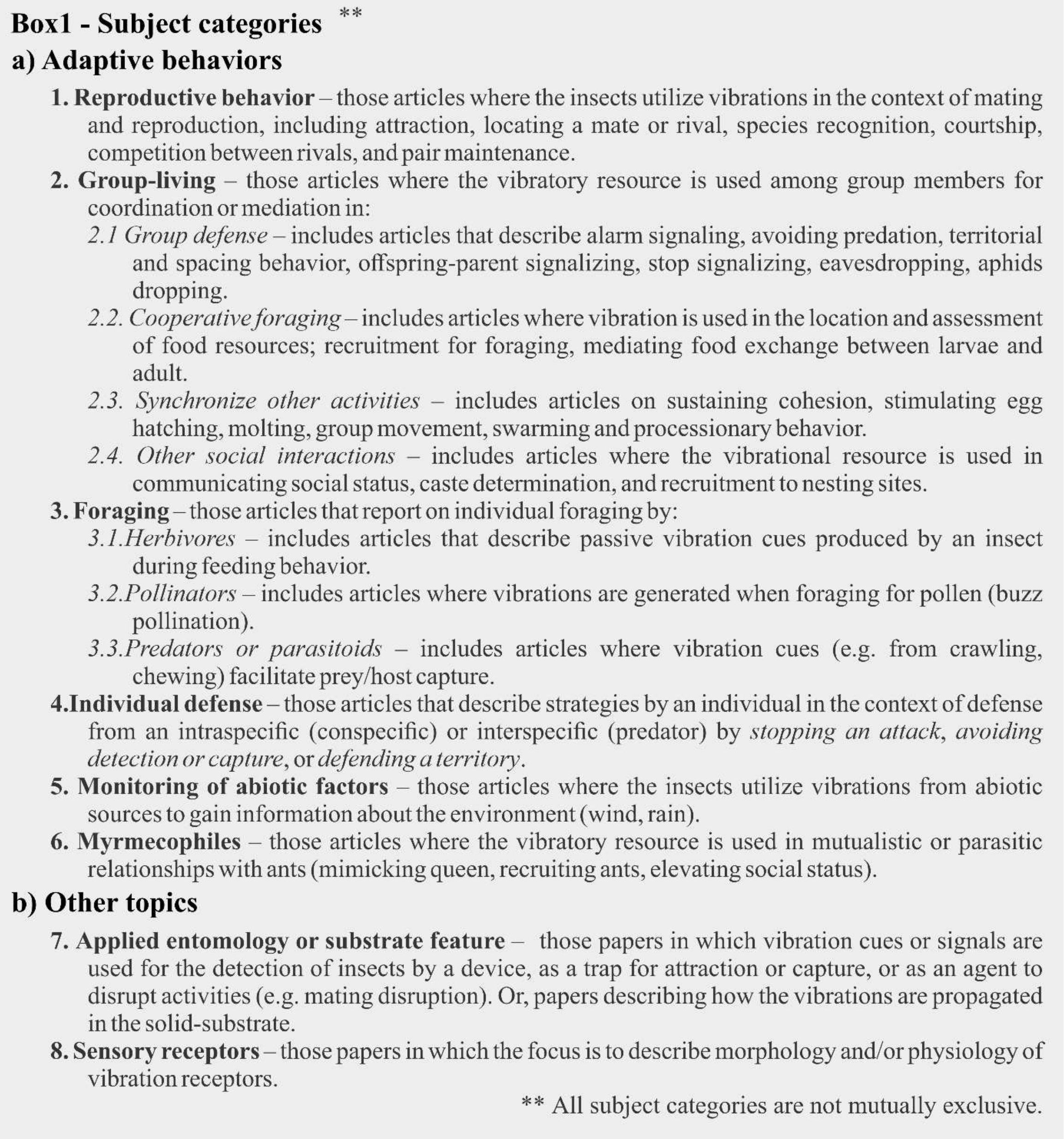


Fig. 1. Flowchart describing how scientific articles were step by step included/excluded in the literature dataset at the four stages of the systematic review process (‘Identification’, ‘Screening’, ‘Eligibility’, and ‘Included’). Refer to the Materials and methods for details on screening and eligibility criteria.

Qualitative analyses

The selected papers were used to recognize overall temporal trends in publishing, and to identify taxonomic groups (i.e., insect orders), developmental stages (i.e., egg, larva, pupa, or adult), and topics studied. Additionally, we compartmentalized the papers within eight subject categories, following the guidelines in Box 1 to recognize the major focus of attention. This information was compiled and summarized (Table S1), and used for building the interaction matrixes, which identified the relationship among subject categories and insect orders tested.



Box1 - Subject categories **

a) Adaptive behaviors

1. **Reproductive behavior** – those articles where the insects utilize vibrations in the context of mating and reproduction, including attraction, locating a mate or rival, species recognition, courtship, competition between rivals, and pair maintenance.
2. **Group-living** – those articles where the vibratory resource is used among group members for coordination or mediation in:
    - *2.1 Group defense* – includes articles that describe alarm signaling, avoiding predation, territorial and spacing behavior, offspring-parent signalizing, stop signalizing, eavesdropping, aphids dropping.
    - *2.2. Cooperative foraging* – includes articles where vibration is used in the location and assessment of food resources; recruitment for foraging, mediating food exchange between larvae and adult.
    - *2.3. Synchronize other activities* – includes articles on sustaining cohesion, stimulating egg hatching, molting, group movement, swarming and processionary behavior.
    - *2.4. Other social interactions* – includes articles where the vibrational resource is used in communicating social status, caste determination, and recruitment to nesting sites.
3. **Foraging** – those articles that report on individual foraging by:
    - *3.1.Herbivores* – includes articles that describe passive vibration cues produced by an insect during feeding behavior.
    - *3.2.Pollinators* – includes articles where vibrations are generated when foraging for pollen (buzz pollination).
    - *3.3.Predators or parasitoids* – includes articles where vibration cues (e.g. from crawling, chewing) facilitate prey/host capture.
4. **Individual defense** – those articles that describe strategies by an individual in the context of defense from an intraspecific (conspecific) or interspecific (predator) by *stopping an attack*, *avoiding detection or capture*, or *defending a territory*.
5. **Monitoring of abiotic factors** – those articles where the insects utilize vibrations from abiotic sources to gain information about the environment (wind, rain).
6. **Myrmecophiles** – those articles where the vibratory resource is used in mutualistic or parasitic relationships with ants (mimicking queen, recruiting ants, elevating social status).

b) Other topics

7. **Applied entomology or substrate feature** – those papers in which vibration cues or signals are used for the detection of insects by a device, as a trap for attraction or capture, or as an agent to disrupt activities (e.g. mating disruption). Or, papers describing how the vibrations are propagated in the solid-substrate.
8. **Sensory receptors** – those papers in which the focus is to describe morphology and/or physiology of vibration receptors.

** All subject categories are not mutually exclusive.

Box 1. Definitions of subject categories used to systematize papers about vibratory sensing and communication in insects.

Quantitative analyses

To establish the dataset for the quantitative analyses, papers were selected for inclusion based on two eligibility criteria: (i) the vibration should mediate at least one behavior with an adaptive role, according to the subject categories established in the Box 1, and (ii) each behavioral context should contain at least two taxonomic orders and three papers published, which is an assumption to proceed with meta-analyses. This dataset was subjected to meta-analyses with binary outcomes to test specifically whether the publications favored a particular developmental stage and whether there was evidence for vibration reception in an adaptive context, considering as evidence a change in behavior of the receiving organism. In all cases, the taxonomic groups and the adaptive behaviors were used as moderators. The risk ratio and 95% confidence intervals were used to determine the overall effect measured, where the former (i.e., risk ratio, RR) is the likelihood of an outcome between two alternatives (RR = 1 means a similar outcome among two possibilities or lack of bias). The random-effect model was used because the individual studies differ, and their effects are usually assumed to be heterogeneous. The quantification and heterogeneity-test (i.e., Q, H, and I^2) were conducted, and the inverse variance and DerSimonian–Laird methods were used to estimate the between-study variance (τ^2). Studies with $n \leq 1$ event in both groups were excluded from the meta-analyses. All analyses were performed using the R-software version 3.5.1 (R Development Core, Vienna, Austria), with the packages “meta”, “metafor” and “stats” (R Development Core Team 2020; Schwarzer et al. 2015). The graphical illustrations were produced with Wacom creative table (Intuos S, Tokyo, Japan) using Corel Painter (Essential 6, Ottawa, ON, Canada).

Results

Summary of the literature

A summary flowchart showing the results of the article selection procedure is shown in Fig. 1. The original literature search resulted in 4,327 papers from *Web of Science* and *Scopus*. Additionally, 118 papers were incorporated from a comprehensive book on the topic with emphasis on arthropods (Cocroft et al. 2014b), totaling 4,445; 3,019 papers remained after removing duplicates. These 3,019 papers were screened based on titles and abstracts to check for consistency with the criteria of inclusion in the dataset (see Materials and methods for details). This resulted in 831 papers that were used in the qualitative analyses to describe the temporal trends, taxonomic groups, developmental stage, and main subjects explored. To conduct the meta-analyses, two additional eligibility criteria were applied to the 831 papers (see Materials and methods for details) resulting in 547 papers.

Qualitative literature trends

The temporal trend in publishing over a period of 75 years, from January 1945 to December 2020, was followed (Fig. 2A). However, the milestone of the first manuscript published occurred only in the early 1960s, when Moore in 1961, identified vibrations by hemipteran adults (Moore 1961; Table S1). Overall, the trajectory of the field during its two first decades following the first publication in 1961 exhibited a slow linear growth, with studies remaining scarce until the late 1980s and 2000s for adults and juveniles respectively. Afterwards, there was an exponential growth in publication output extending to the present (Fig. 2A).

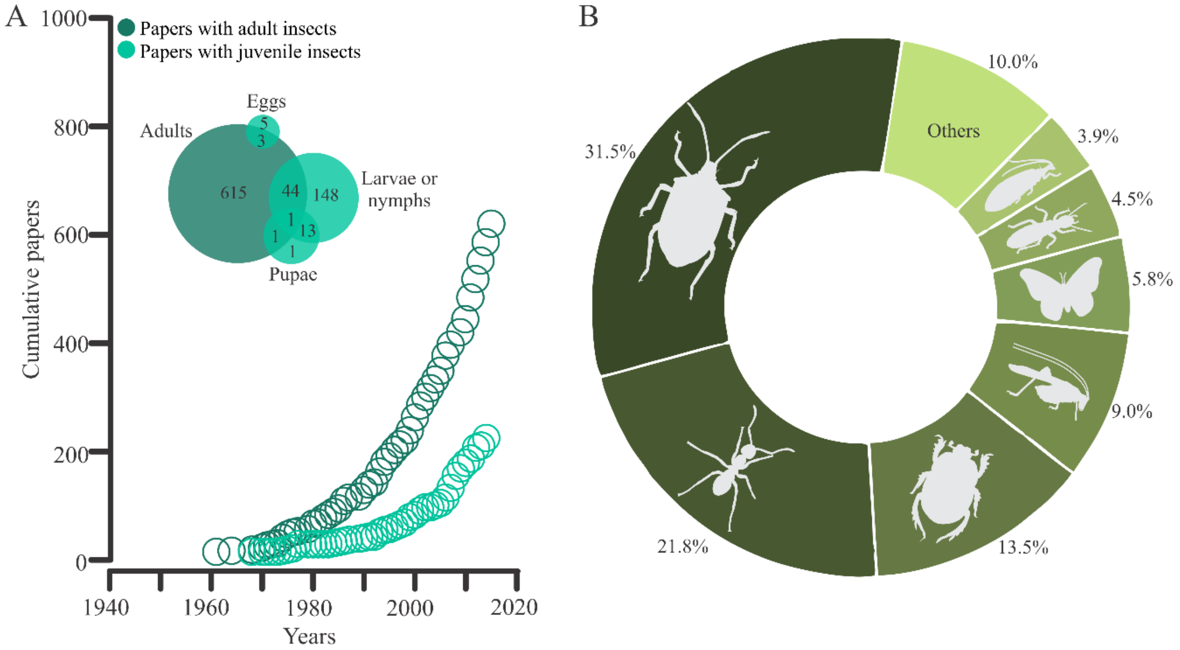


Fig. 2. (A) Scatterplot of the cumulative papers published on solid-borne vibrations of adult (dark green circle) and juvenile (light green circle) insects between 1945-2020. The inner diagram indicates the number of published papers on each specific developmental stage. The overlapping circles in the upper left of the figure indicate papers that include more than one developmental stage. (B) Distribution of the studies on insect solid-borne vibrations among taxonomic insect orders compilated for qualitative analysis (n= 831 papers).

A diversity of taxonomic groups (17 of the 30 recognized orders [Gullan & Cranston 2014, considering Isoptera, Blattodea, Psocoptera, and Phthiraptera as different orders]) was identified in the scientific papers on vibratory sensing and communication. The most representative groups were Hemiptera (31.5%), Hymenoptera (21.8%), Coleoptera (13.5%), Orthoptera (9.0%), Lepidoptera (5.8%), Isoptera (4.5%), and Neuroptera (3.9%), while the ten insect orders remaining encompassed only 10% of papers (Fig. 2B). Orders that were not reported included Archaeognatha, Zygentoma, Ephemeroptera, Zoraptera, Grylloblattodea, Mantodea, Psocoptera, Phthiraptera, Thysanoptera, Raphidioptera, Megaloptera, Strepsiptera, and Siphonaptera.

There was an apparent bias in the developmental stages being studied, with the vast majority of studies focusing on adults (Fig. 2A). Indeed, of 831 papers identified, 74% focused only on adults (n= 615 papers), 20.1% only on juveniles (n= 167 papers), and 5.9% covered both juveniles and adults (n= 49 papers). Among juveniles, the vibration was more frequently investigated on larvae or nymphs (n= 206 papers), while pupae (n= 16 papers) and eggs (n= 8 papers) were least represented (Fig. 2A).

Of the 831 papers, a wide range of topics was identified, extending from adaptive behaviors to applied entomology (see Table S1). Such topics were herein compartmentalized within eight broad subject categories (Box 1) in order to examine the most commonly explored subjects, and the main taxonomic groups studied within each (Fig. 3). Overall, the interaction among taxonomic groups and subject categories showed that about 70.4% of papers focused on understanding the role of vibration in an adaptive context (Fig. 3). These articles were clustered into six subject categories of which the main one is reproductive behavior (36.2% of papers; 12 orders), followed by the moderately represented group-living (17.3% of papers; 6 orders), foraging (9.2% of papers; 7 orders), and individual defense (5.5% of papers; 9 orders); and then the least represented, monitoring abiotic factors (1% of papers; 5 orders) and myrmecophilic interactions (1.2% of papers; 2 orders) (Fig. 3). The remaining 29.6% of the literature did not relate directly to adaptive functions, and these included papers on applied entomology (16.5% of papers; 9 orders) and sensory organs (13.1% of papers; 12 orders) (Fig. 3).

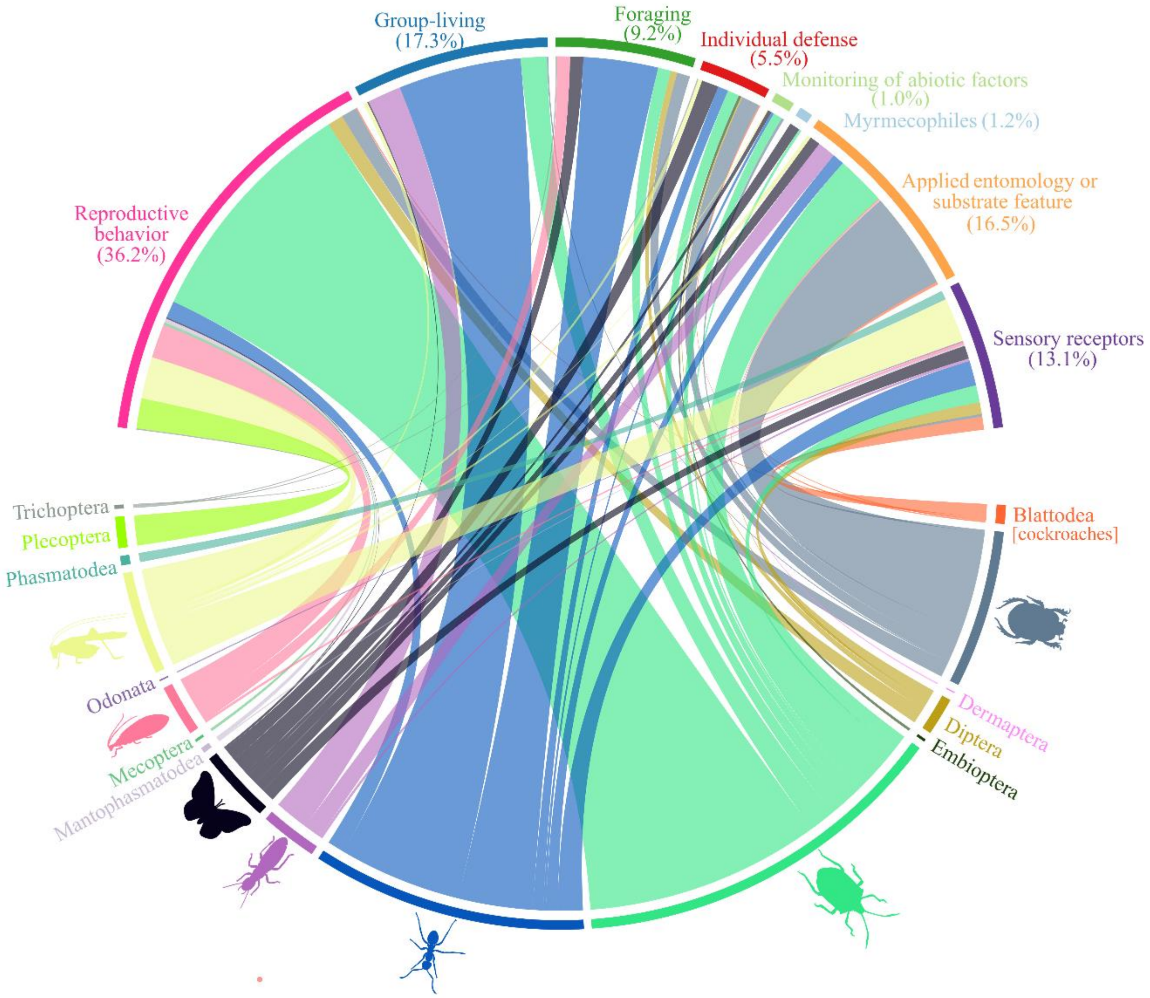


Fig. 3. Interaction diagram between insect orders and subject categories included in the current systematic review from studies documenting vibratory sensing and communication in insects (n=831 papers). Connections between insect orders and subject categories represent the interaction. The thickness of arcs represents the number of times that interactions were studied.

In summary, a total of 831 papers were selected for qualitative analysis. This qualitative description of the literature showed an increase in studies on vibratory sensing and communication in insects during the last 75 years. Reports included 17 insect orders, with a heavy focus on the adult stage. The papers focused mainly on adaptive behaviors, with reproductive behaviors representing the topic most commonly studied among subject categories.

Meta-analyses and overall trends

Of the 831 studies, 547 met the two eligibility criteria for meta-analyses (see Materials and methods). These 547 papers covered four subjects related to adaptive behavior: reproductive behavior (7 orders), group-living (3 orders), foraging (6 orders), and individual defense (4 orders). These papers were subjected to meta-analyses to test two main questions.

The first question was if there is a bias towards a developmental stage. The meta-analysis model indicated that indeed the likelihood of studies with adults is about 3x higher than with juveniles (RR= 3.01; z= 2.54; $P< 0.01$; orange diamond) (Fig. 4), reinforcing the trends previously suggested in the qualitative analysis. However, the dataset indicates that the likelihood of studies in favor of a specific development stage is strongly related to the taxonomic group and adaptive behavior, reflected in high and significant heterogeneity among studies, which deserves scrutiny (Fig. 4). Studies on reproductive behavior are highly associated with adults regardless of the taxonomic group (RR=50.16; I^2= 0%; P=0.84; pink diamond), which is expected. On the other hand, group-living (RR=0.73; I^2= 93%; $P< 0.01$; blue diamond), individual foraging (RR=0.84; I^2= 79%; $P< 0.01$; green diamond) and individual defense (RR=1.44; I^2= 70%; P< 0.01; red diamond) do not exhibit bias towards any specific developmental stage. In these cases, the developmental stage studied is strongly associated with the insect orders; for instance, Isoptera, Lepidoptera, and Neuroptera are more commonly studied as juveniles, whereas the remaining orders are predominantly studied as adults (Fig. 4).

Meta-analysis was also used to ask whether there is supporting evidence for vibration being confirmed to serve an adaptive function. The likelihood of studies documenting a receiver response was 2x higher (RR= 2.13; z= 2.47; P= 0.01; orange diamond) than not. Nonetheless, the dataset exhibits high heterogeneity among insect orders and behavioral contexts, which invites further scrutiny within each behavioral context (Fig. 5). Reproductive behavior (RR= 5.44; I^2= 82%; P= 0.01; pink diamond) and group-living (RR= 2.80; I^2= 76%; P= 0.01; blue diamond) are prevalent among the receiver responses recorded, regardless of insect order. In contrast, individual foraging (RR=0.54; I^2= 71%; $P< 0.01$; green diamond) and individual defense (RR=1.34; I^2= 81%; $P< 0.01$; red diamond) do not exhibit significant trends (RR around 1), and thus show similar likelihood in reporting adaptive consequences of the response. Besides, the assessment of response is strongly related to the insect order investigated (Fig. 5).

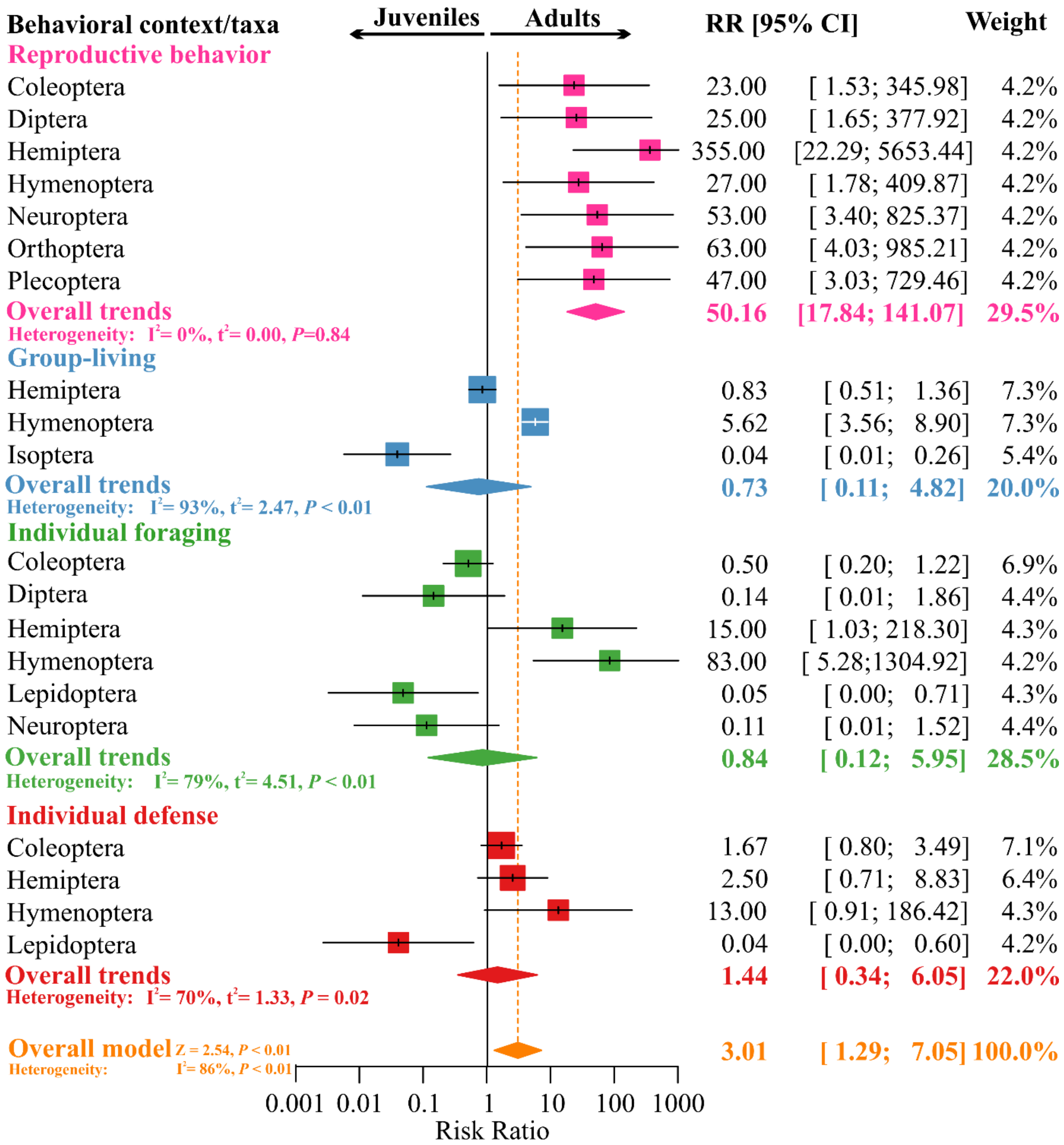


Fig. 4. Forest plot summarizing the results from the frequency of studies by developmental stages, considering the insect orders and behavioral contexts, as moderators. The risk ratios (95% CIs) are denoted by colored boxes (horizontal black lines). The combined RR estimate for overall trends is represented by a colored diamond, where diamond width corresponds to 95% CI bounds. The black vertical solid-line represents lack of effect, whereas the vertical orange dashed line shows the overall estimated effect resulting from all studies. The *P*-values for heterogeneity test are indicated.

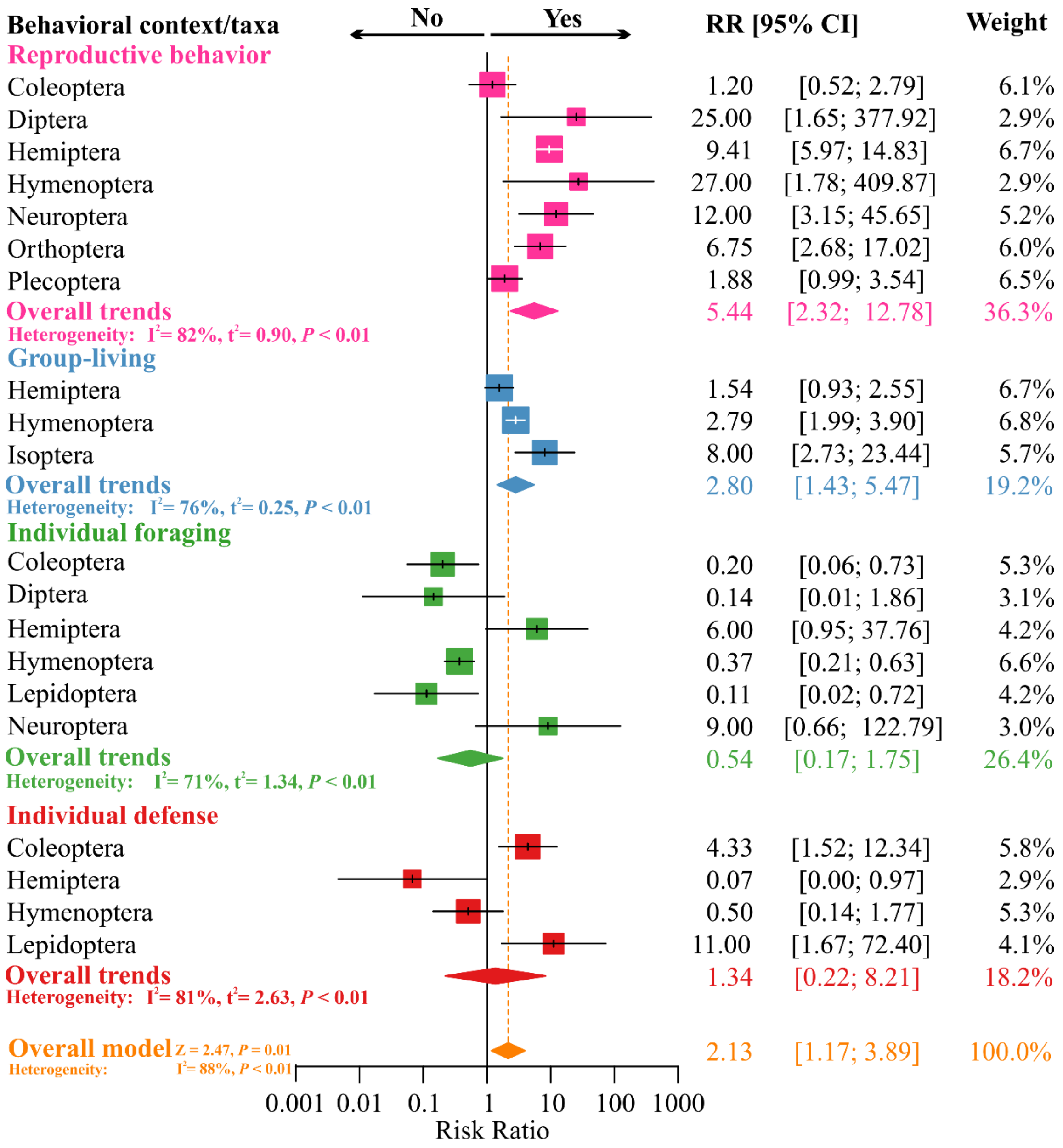


Fig. 5. Forest plot summarizing the results from the frequency of studies documenting a response to vibration by the receiving organism, considering the insect order and behavioral contexts as moderators. The risk ratios (95% CIs) are denoted by colored boxes (horizontal black lines). The combined RR estimate for overall trends is represented by a colored diamond, where diamond width corresponds to 95% CI bounds. The black vertical solid-line represents lack of effect, whereas the orange vertical dashed line shows the overall estimated effect resulting from all studies. The *P*-values for the heterogeneity test are indicated.

In summary, the quantitative analyses of the literature confirmed bias in the developmental stage, revealing a likelihood of studies 3x higher with adults than with juveniles. Also, scientific papers often document a response or change in behavior in the receiving organism, supporting the conclusion that the studies provided experimental evidence for the function of vibration in adaptive contexts. However, these studies are mainly related to reproduction and group living. It is also important to note that only a limited number of insect orders (9 of 17 orders identified to be associated with vibrations) have been studied experimentally in the context of adaptive function.

Discussion

In rapidly growing subjects some aspects of research are more extensively explored than others. This study provides a systematic review and meta-analyses of published literature on vibratory sensing and communication in insects with the goals to summarize the growth of this topic over the past 75 years, and to identify and quantify the trends and biases within the field that will help to guide future research.

Our results showed that there was an exponential growth in the field beginning in the late 1980s through to the present. The earliest reports related to substrate-borne vibrations in insects were published a century ago, in the 1920s (e.g., booklice: Pearman 1928; termites: Emerson & Simpson 1929). However, such reports are not included in our literature review, which extended from 1945 to 2020 due to limitations on the time period covered by the databases. The scientific publication output on vibratory sensing and communication in insects began modestly in the early 1960s, with studies remaining scarce until the late 1980s. The low publication rate during this early period was expected, as the scientific community had limited access to technologies necessary to detect vibrations, relying primarily on phonograph cartridges (Muraoka et al. 1974; Watanabe 1978). In the late 1980s technological advances increased the availability of equipment (e.g., accelerometers, laser doppler vibrometers) and consequently, the awareness of this sensory modality (Cocroft & Rodríguez 2005; Elias and Mason 2014). Such advances allowed for a rapid expansion of research on the subject of insect biotremology, resulting in a total of 831 papers included in our literature survey. The exponential trend currently persists, as 96 new papers were identified in the Web of Science database subsequent to our search (i.e., between December 2020 and August 2021). This ongoing publication output likely reflects the increase of researcher networks around the world, the broadening of topics addressed in the research field, and the increasing accessibility to instrumentation.

In our survey, we identified which insect orders included species that detect or generate vibration. The number of 17 insect orders recorded (see Fig. 3) was lower than the 18 orders previously reported by Cocroft & Rodriguez (2005), a likely consequence of our more restrictive criteria of assessment. Curiously, the orders identified did not overlap entirely between the two studies. For example, Raphidioptera, Megaloptera, Psocoptera, Thysanoptera, and Zoraptera, were reported by Cocroft & Rodrigues (2005), but not identified herein. In contrast, Odonata, Dermaptera, Phasmatodea, and Mantophasmatodea, identified in our survey, were not identified by Cocroft & Rodrigues (2005). This discrepancy is likely due to the different methodological approaches used to identify the literature (i.e., narrative review vs systematic reviews [see Uman 2011; Gurevitch et al. 2018]) and the ~15-year gap between the two studies. Regardless, our results reinforce the statement that we remain in the process of "identifying the players", including taxa never considered before (Hill 2008; Yack 2016), as at least 13 orders (our study), or 8 if we include those additional orders identified by Cocroft & Rodrigues (2005), remain unreported in the literature.

Among the 17 insect orders we identified, the seven with most published papers were Hemiptera, Hymenoptera, Coleoptera, Orthoptera, Lepidoptera, Isoptera, and Neuroptera, respectively (Fig. 2B). This bias was expected, as these orders also have a large number of species described, and are also well-studied for other reasons (Gullan & Cranston 2014), thereby increasing the likelihood of researchers noticing vibratory behaviors. In contrast, the other 10 orders identified were only sparsely represented (Fig. 3). Future studies should focus on the orders not well-represented in the literature, and also should explore sparsely represented genera, families, and species from all orders. This will reveal a wider use of vibration within the Class Insecta and allow for comparative studies to test hypotheses on function and evolution.

Our results confirmed that there is a research bias towards adults rather than juveniles (Fig. 4). This result reinforces the trends of our own qualitative analysis, as well as previous narrative reviews (e.g., Virant-Doberlet & Čokl 2004; Hill & Wessel 2016; Yack 2016). Possible explanations for this bias may be the relatively smaller size of juveniles, making vibrations less easily detectable, as well as the general research interest on reproduction in many orders (Fig. 4-pink diamond), which of course is absent in juveniles. The bias in favor of adults was not generalized among all behavioral contexts. A similar likelihood of studies with adults and juveniles (or lack of bias, RR=1) exists for group-living (Fig. 4 - blue diamond), foraging (Fig. 4 - green diamond), and individual defense contexts (Fig. 4 - red diamond) showing that studies with juveniles, although smaller in number, are better distributed among these behavioral contexts. This result is likely associated with a growing number of reports that juveniles (particularly from Isoptera, Lepidoptera, Neuroptera, and Hemiptera) use vibrations in a variety of contexts, including egg hatching synchronization (Mukai et al. 2014; Nishide & Tanaka 2016; Endo et al. 2019), coordination of social group activities and recruitment (Fletcher 2007; 2008; Hamel & Cocroft 2012; Yadav et al. 2017), foraging (Suryanarayanan & Jeanne 2008; Suryanarayanan et al. 2011), territorial and spacing behavior (Yack et al. 2001; 2014; Fletcher et al. 2006; Scott et al. 2010; Guedes et al. 2012), and predator avoidance (Castellanos & Barbosa 2006; Low 2008; Gish et al. 2012; Kojima et al. 2012a). This result highlights the potential of juveniles as experimental models in biotremology. Juveniles also comprise a remarkably large portion of agricultural pests, making them conspicuous research models for basic and applied entomology.

Our survey identified a diversity of topics related to insects and vibration, ranging from communication to pest management applications. There was a prevalence of papers focusing on reproductive behaviors, group living, and applied entomology, and a strong interaction between these topics and Hemiptera, Hymenoptera, and Coleoptera, respectively, which suggested that topic and taxonomic biases are related (Fig. 3). The hemipterans, for instance, were important experimental models since the pioneering works of Ossiannilsson (1949), Strübing (1958), Gogala et al. (1974), and Ichikawa & Ishii (1974), leading to a historical series of publications on behaviors associated with reproduction such as species recognition, attraction, mate finding, courtship, and rivalry. The hymenopterans are also conspicuous models in studies of group activities mediated by vibration, such as when eusocial bees signal the location and profitability of a food source (e.g., Hrncir et al. 2004a; 2004b), or when sawfly larvae use vibrations for recruitment and group cohesion (e.g., Fletcher 2007; 2008). Coleopterans have commonly been used as models for applied entomology from 1965 to the present (Bailey & McCabe 1965; Mankin et al. 2021), with a focus on the detection and monitoring of concealed insects through vibroacoustic cues (e.g., stored product weevils [Njoroge et al. 2016] and wood-boring beetles [Mankin et al. 2016; Jalinas et al. 2019]) (see TableS1).

We assessed whether studies provided evidence for adaptive significance, based on whether there was evidence for a receiver response to a vibrational cue or signal. Our findings revealed that the likelihood of studies documenting a receiver response was 2x higher than not (Fig. 5). Such results were more prominent in reproductive behaviors and group living. This likely reflects the easier assessment of these behaviors, such as when stinkbugs move towards a signaling mate (Čokl & Virant-Doberlet 2003) or when termites respond to an alarm call (Rosengaus et al. 1999; Delattre et al. 2019). In contrast, studies of foraging and individual defense showed no bias in documenting an adaptive behavior (i.e., they were equally likely to report an adaptive behavior or not).

The lack of bias in foraging likely reflects the fact that, while in some cases a receiver response is relatively easy to document, such as when a predator detects and responds to vibration cues of a prey (e.g., walking or chewing), or by detecting its own signals (e.g., vibrational sounding/echolocation) (Devetak 1985; Pfannenstiel et al. 1995; Meyhöfer et al. 1997; Al-Wahaibi & Walker 2000; Broad & Quicke 2000; Devetak et al. 2007; Fertin & Casas 2007), in other cases a change in behavior of the receiver was not always evident. For example, evidence for a response of the receiver is not always reported in examples of foraging activities such as in buzz pollination, when bees actively vibrate a flower's anthers to release pollen (King 1993; De-Luca et al. 2019; Rosi-Denadai et al. 2020), or when ants create a "vibratome" to facilitate leaf cutting (Tautz et al. 1995). While such examples still constitute adaptive behaviors, they were not scored as such based on our criteria. Similarly, in examples of individual defense, in some cases evidence for vibration reception is easier to document, such as when an insect responds to an attack or threat (Kojima et al. 2012a; 2012b, 2012c; Ichikawa & Sakamoto 2013; Ben-Ari et al. 2014), defends a territory (Yack et al. 2001; 2014; Fletcher et al. 2006; Bowen et al. 2008; Scott et al. 2010; Scott & Yack 2012), or avoids detection by freezing or thanatosis (Acheampong & Mitchell 1997; Djemai et al. 2004; Castellanos & Barbosa 2006; Jabłoński & Lee 2006; Takanashi et al. 2016; Miyatake et al. 2019). On the other hand, many other articles commonly reporting a defensive behavior do not provide evidence of information transfer (Masters 1979; 1980; Puranik et al. 1981; Masters et al. 1983; Tschuch & Brothers 1999; Quiroga et al. 2019), and thus do not test for potential adaptive roles.

In conclusion, our literature survey recognized 17 insect orders associated with vibratory events that are used in a wide diversity of contexts. In these studies, three prominent biases were detected: i) prevalence of studies on Hemiptera, Hymenoptera, and Coleoptera; and ii) a focus on adults, with far less attention to juveniles; and iii) on reproductive behaviors, with less attention to other behavioral contexts. Future studies should focus on a broader range of orders and higher taxa (i.e., genera, families, species). Documentation of the role of vibration in different adaptive contexts is also necessary in exploring how both adults and juveniles (i.e., eggs, larvae/nymphs, and pupae) use vibrations. A lack of research on the vibratory landscapes of most insects remains noticeable, and also importantly, how many insects sense and process vibrations. Such studies will no doubt lead to novel and intriguing insights into the complex vibratory environments of substrate-bound insects and may have practical applications for monitoring and managing pests, and inspiring biomimetic devices.

Supplementary information

Table S1: Listed of retrieved articles and their respective summaries that were used for result survey and meta-analyses. Supplementary file available in: http://tiny.cc/zzrkuz

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References

Acheampong, S., & Mitchell, B. K. (1997). Quiescence in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, 82(1), 83-89. https://doi.org/10.1046/j.1570-7458.1997.00116.x

Adedeji, A.A., Ekramirad, N., Rady, A., Hamidisepehr, A., Donohue, K.D., Villanueva, R.T., Parrish, C.A., & Li, M. (2020). Non-destructive technologies for detecting insect infestation in fruits and vegetables under postharvest conditions: a critical review. *Foods*, 9(7), 927. https://doi.org/10.3390/foods9070927

Al-Wahaibi, A. K., & Walker, G. P. (2000). Oviposition behavior of *Anagrus nigriventris*, an egg parasitoid of beet leafhopper, *Circulifer tenellus*. *BioControl*, 45(2), 139-153. https://doi.org/10.1023/A:1009994405237

Bailey, S. W., & McCabe, J. B. (1965). The detection of immature stages of insects within grains of wheat. *Journal of Stored Products Research*, 1(2), 201-202. https://doi.org/10.1016/0022-474X(65)90022-6

Banga, K. S., Kotwaliwale, N., Mohapatra, D., & Giri, S. K. (2018). Techniques for insect detection in stored food grains: An overview. *Food Control*, 94(1), 167-176. https://doi.org/10.1016/j.foodcont.2018.07.008

Ben-Ari, M., Talal, S., & Inbar, M. (2014). Anticipatory and reactive crouching of pea aphids in response to environmental perturbations. *Environmental Entomology*, 43(5), 1319-1326. https://doi.org/10.1603/EN14046

Bowen, J. L., Mahony, S. J., Mason, A. C., & Yack, J. E. (2008). Vibration-mediated territoriality in the warty birch caterpillar *Drepana bilineata*. *Physiological Entomology*, 33(3), 238-250. https://doi.org/10.1111/j.1365-3032.2008.00627.x

Broad, G. R., & Quicke, D. L. (2000). The adaptive significance of host location by vibrational sounding in parasitoid wasps. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1460), 2403-2409. https://doi.org/10.1098/rspb.2000.1298

Casacci, L. P., Bonelli, S., Balletto, E., & Barbero, F. (2019). Multimodal signaling in myrmecophilous butterflies. *Frontiers in Ecology and Evolution*, 7, 454. https://doi.org/10.3389/fevo.2019.00454

Casas, J., & Magal, C. (2006). Mutual eavesdropping through vibrations in a host-parasitoid interaction: from plant biomechanics to behavioural ecology. In S. Drosopoulos, & M.F. Claridge (Eds.), *Insect sounds and communication: Physiology, Behaviour, Ecology, and Evolution*, (pp. 263–271). Boca Raton, Florida: CRC Press.

Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, 72(2), 461-469. https://doi.org/10.1016/j.anbehav.2006.02.005

Claridge, M. F. (1985). Acoustic signals in the Homoptera: behavior, taxonomy, and evolution. *Annual Review of Entomology*, 30(1), 297-317. https://doi.org/10.1146/annurev.en.30.010185.001501

Cocroft, R. B. (2001). Vibrational communication and the ecology of group-living, herbivorous insects. *American Zoologist*, 41(5), 1215-1221. https://doi.org/10.1093/icb/41.5.1215

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, 55(4), 323-334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO,2

Cocroft, R. B., & McNett, G. D. (2006). Vibratory communication in treehoppers (Hemiptera: Membracidae). In S. Drosopoulos, & M. F. Claridge (Eds.), *Insect sounds and communication: Physiology, Behaviour, Ecology, and Evolution*, (pp. 305-318). Boca Raton, Florida: CRC Press.

Cocroft, R. B., Gogala, M., Hill, P. S., & Wessel, A. (2014a). Fostering research progress in a rapidly growing field. In R. B. Cocroft, M. Gogala, P.S.M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. 3-12). Heidelberg, Berlin: Springer. https://doi.org/10.1007/978-3-662-43607-3_1

Cocroft, R. B., Gogala, M., Hill, P. S. M., & Wessel, A. (2014b). *Studying vibrational communication*, Springer. https://doi.org/10.1007/978-3-662-43607-3

Čokl, A., & Virant-Doberlet, M. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annual Review of Entomology*, 48(1), 29-50. https://doi.org/10.1146/annurev.ento.48.091801.112605

Delattre, O., Šobotník, J., Jandák, V., Synek, J., Cvačka, J., Jiříček, O., Bourguignon, T., & Sillam-Dussès, D. (2019). Chemical and vibratory signals used in alarm communication in the termite

Reticulitermes flavipes (Rhinotermitidae). *Insectes Sociaux*, 66(2), 265-272. https://doi.org/10.1007/s00040-018-00682-9

De-Luca, P. A., & Vallejo-Marin, M. (2013). What's the 'buzz'about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology*, 16(4), 429-435. https://doi.org/10.1016/j.pbi.2013.05.002

De-Luca, P. A., Buchmann, S., Galen, C., Mason, A. C., & Vallejo-Marín, M. (2019). Does body size predict the buzz-pollination frequencies used by bees? *Ecology and Evolution,* 9(8), 4875-4887. https://doi.org/10.1002/ece3.5092

Devetak, D. (1985). Detection of substrate vibrations in the antlion larva, *Myrmeleon formicarius* (Neuroptera: Myrmeleonidae). *Biološki vestnik*, 33(2), 11-22.

Devetak, D. (1998). Detection of substrate vibration in Neuropteroidea: a review. *Acta Zoologica Fennica*, 209, 87-94.

Devetak, D., Mencinger-Vračko, B., Devetak, M., Marhl, M., & Špernjak, A. (2007). Sand as a medium for transmission of vibratory signals of prey in antlions *Euroleon nostras* (Neuroptera: Myrmeleontidae). *Physiological Entomology*, 32(3), 268-274. https://doi.org/10.1111/j.1365-3032.2007.00580.x

Djemai, I., Casas, J., & Magal, C. (2004). Parasitoid foraging decisions mediated by artificial vibrations. *Animal Behaviour*, 67(3), 567-571. https://doi.org/10.1016/j.anbehav.2003.07.006

Eberhard, M. J., & Eberhard, S. H. (2013). Evolution and diversity of vibrational signals in Mantophasmatodea (Insecta). *Journal of Insect Behavior*, 26(3), 352-370. https://doi.org/10.1007/s10905-014-9472-2

Elias, D. O., & Mason, A. C. (2014). The role of wave and substrate heterogeneity in vibratory communication: practical issues in studying the effect of vibratory environments in communication. In R. B. Cocroft, M. Gogala, P.S.M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. 215–247). Heidelberg, Berlin: Springer. https://doi.org/10.1007/978-3-662-43607-3_12

Emerson, A. E., & Simpson, R. C. (1929). Apparatus for the detection of substratum communication among termites. *Science*, 69(1799), 648-649. https://doi.org/10.1126/science.69.1799.648

Endler, J.A. (2014). The emerging field of tremology. In R. B. Cocroft, M. Gogala, P.S.M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. vii–x). Heidelberg, Berlin: Springer. https://doi.org/10.1007/978-3-662-43607-3

Endo, J., Takanashi, T., Mukai, H., & Numata, H. (2019). Egg-cracking vibration as a cue for stink bug siblings to synchronize hatching. *Current Biology*, 29(1), 143-148. https://doi.org/10.1016/j.cub.2018.11.024

Fertin, A., & Casas, J. (2007). Orientation towards prey in antlions: efficient use of wave propagation in sand. *Journal of Experimental Biology*, 210(19), 3337-3343. https://doi.org/10.1242/jeb.004473

Fletcher, L. E., Yack, J. E., Fitzgerald, T. D., & Hoy, R. R. (2006). Vibrational communication in the cherry leaf roller caterpillar *Caloptilia serotinella* (Gracillarioidea: Gracillariidae). *Journal of Insect Behavior*, 19(1), 1-18. https://doi.org/10.1007/s10905-005-9007-y

Giunti, G, Camolo, O., Laudani, F., & Palmeri, V. (2018) Male courtship behaviour and potential for female mate choice in the black soldier fly *Hermetia illucens* L. (Diptera: Stratiomyidae). *Entomologia Generalis*, 38(1): 29-46. https://doi.org/10.1127/entomologia/2018/0657

Fletcher, L. E. (2007). Vibrational signals in a gregarious sawfly larva (*Perga affinis*): group coordination or competitive signaling?. *Behavioral Ecology and Sociobiology*, 61(12), 1809-1821. https://doi.org/10.1007/s00265-007-0414-2

Fletcher, L. E. (2008). Cooperative signaling as a potential mechanism for cohesion in a gregarious sawfly larva, *Perga affinis*. *Behavioral Ecology and Sociobiology*, 62(7), 1127-1138. https://doi.org/10.1007/s00265-007-0541-9

Gish, M., Dafni, A., & Inbar, M. (2012). Young aphids avoid erroneous dropping when evading mammalian herbivores by combining input from two sensory modalities. *PLoS One*, 7(4), e32706. https://doi.org/10.1371/journal.pone.0032706

Gogala, M., Čokl, A., Drašlar, K., & Blaževič, A. (1974). Substrate-borne sound communication in Cydnidae (Heteroptera). *Journal of Comparative Physiology A*, 94, 25–31. https://doi.org/10.1007/BF00610155

Guedes, R. N. C., Matheson, S. M., Frei, B., Smith, M. L., & Yack, J. E. (2012). Vibration detection and discrimination in the masked birch caterpillar (*Drepana arcuata*). *Journal of Comparative Physiology A*, 198(5), 325-335. https://doi.org/10.1007/s00359-012-0711-8

Gullan, P.J., & Cranston, P.S. (2014). *The insects: An outline of Entomology,* John Wiley & Sons Ltd.

Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, 555(7695), 175-182. https://doi.org/10.1038/nature25753

Hamel, J. A., & Cocroft, R. B. (2012). Negative feedback from maternal signals reduces false alarms by collectively signalling offspring. *Proceedings of the Royal Society B: Biological Sciences*, 279(1743), 3820-3826. https://doi.org/10.1098/rspb.2012.1181

Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., & Mochizuki, A. (2012). Parallel evolution in courtship songs of North American and European green lacewings (Neuroptera: Chrysopidae). *Biological Journal of the Linnean Society*, 105(4), 776-796. https://doi.org/10.1111/j.1095-8312.2011.01845.x

Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., & Mochizuki, A. (2013). Obligatory duetting behaviour in the *Chrysoperla carnea*-group of cryptic species (Neuroptera: Chrysopidae): its role in shaping evolutionary history. *Biological Reviews*, 88(4), 787-808. https://doi.org/10.1111/brv.12027

Hill, P.S.M. (2008). *Vibrational communication in animals*. Harvard University Press.

Hill, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften*, 96(12), 1355-1371. https://doi.org/10.1007/s00114-009-0588-8

Hill, P. S., & Wessel, A. (2016). Biotremology. *Current Biology*, 26(5), R187-R191. https://doi.org/10.1016/J.CUB.2016.01.054

Hill, P.S.M., Lakes-Harlan, R., Mazzoni, V., Narins, P.M., Virant-Doberlet, M., & Wessel, A. (2019). *Biotremology: Studying vibrational behavior*, Springer. https://doi.org/10.1007/978-3-030-22293-2

Hrncir, M., Jarau, S., Zucchi, R., & Barth, F. G. (2004a). Thorax vibrations of a stingless bee (*Melipona seminigra*). I. No influence of visual flow. *Journal of Comparative Physiology A*, 190(7), 539-548. https://doi.org/10.1007/s00359-004-0514-7

Hrncir, M., Jarau, S., Zucchi, R., & Barth, F. G. (2004b). Thorax vibrations of a stingless bee (*Melipona seminigra*). II. Dependence on sugar concentration. *Journal of Comparative Physiology A*, 190(7), 549–560. https://doi.org/10.1007/s00359-004-0515-6

Hunt, J. H., & Richard, F. J. (2013). Intracolony vibroacoustic communication in social insects. *Insectes Sociaux*, 60(4), 403-417. https://doi.org/10.1007/s00040-013-0311-9

Ichikawa, T., & Ishii, S. (1974) Mating signal of the brown planthopper, *Nilaparvata lugens* Stål (Homoptera: Delphacidae): vibration of the substrate. *Applied Entomology and Zoology*, 9(3), 196-198. https://doi.org/10.1303/aez.9.196

Ichikawa, T., & Sakamoto, H. (2013). A third type of defensive behavior in the tenebrionid beetle *Zophobas atratus* pupae. *Journal of Insect Science*, 13(1), 33. https://doi.org/10.1673/031.013.3301

Jabłoński, P. G., & Lee, S. D. (2006). Effects of visual stimuli, substrate-borne vibrations and air current stimuli on escape reactions in insect prey of flush-pursuing birds and their implications for evolution of flush-pursuers. *Behaviour*, 143, 303-324. https://doi.org/10.1163/156853906775897860

Jalinas, J., Güerri-Agulló, B., Dosunmu, O. G., Haseeb, M., Lopez-Llorca, L. V., & Mankin, R. W. (2019). Acoustic signal applications in detection and management of *Rhynchophorus* spp. in fruit-crops and ornamental palms. *Florida Entomologist*, 102(3), 475-479. https://doi.org/10.1653/024.102.0303

King, M. J. (1993). Buzz foraging mechanism of bumble bees. *Journal of Apicultural Research*, 32(1), 41-49. https://doi.org/10.1080/00218839.1993.11101286

Kojima, W., Ishikawa, Y., & Takanashi, T. (2012a). Deceptive vibratory communication: pupae of a beetle exploit the freeze response of larvae to protect themselves. *Biology Letters*, 8(5), 717-720. https://doi.org/10.1098/rsbl.2012.0386

Kojima, W., Ishikawa, Y., & Takanashi, T. (2012b). Pupal vibratory signals of a group-living beetle that deter larvae: Are they mimics of predator cues?. *Communicative & Integrative Biology*, 5(3), 262-264. https://doi.org/10.4161/cib.19886

Kojima, W., Takanashi, T., & Ishikawa, Y. (2012c). Vibratory communication in the soil: pupal signals deter larval intrusion in a group-living beetle *Trypoxylus dichotoma*. *Behavioral Ecology and Sociobiology*, 66(2), 171-179. https://doi.org/10.1007/s00265-011-1264-5

Lima, M. C. F., de Almeida Leandro, M. E. D., Valero, C., Coronel, L. C. P., & Bazzo, C. O. G. (2020). Automatic detection and monitoring of insect pests—a review. *Agriculture*, 10(5), 161. https://doi.org/10.3390/agriculture10050161

Liu, H., Lee, S. H., & Chahl, J. S. (2017). A review of recent sensing technologies to detect invertebrates on crops. *Precision Agriculture*, 18(4), 635-666. https://doi.org/10.1007/s11119-016-9473-6

Low, C. (2008). Seismic behaviors of a leafminer, *Antispila nysaefoliella* (Lepidoptera: Heliozelidae). *Florida Entomologist*, 91(4), 604-609. https://doi.org/10.1653/0015-4040-91.4.604

Mankin, R. W., Al-Ayedh, H. Y., Aldryhim, Y., & Rohde, B. (2016). Acoustic detection of *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) and *Oryctes elegans* (Coleoptera: Scarabaeidae) in *Phoenix dactylifera* (Arecales: Arecacae) trees and offshoots in Saudi Arabian orchards. *Journal of Economic Entomology*, 109(2), 622-628. https://doi.org/10.1093/jee/tov398

Mankin, R., Hagstrum, D., Guo, M., Eliopoulos, P., & Njoroge, A. (2021). Automated applications of acoustics for stored product insect detection, monitoring, and management. *Insects*, 12(3), 259. https://doi.org/10.3390/insects12030259

Masters, W. M. (1979). Insect disturbance stridulation: its defensive role. *Behavioral Ecology and Sociobiology*, 5, 187-200. https://doi.org/10.1007/BF00293305

Masters, W. M. (1980). Insect disturbance stridulation: characterization of airborne and vibrational components of the sound. *Journal of Comparative Physiology*, 135(3), 259-268. https://doi.org/10.1007/bf00657254

Masters, W. M., Tautz, J., Fletcher, N. H., & Markl, H. (1983). Body vibration and sound production in an insect (*Atta sexdens*) without specialized radiating structures. *Journal of Comparative Physiology*, 150(2), 239-249. https://doi.org/10.1007/bf00606374

Maynard-Smith, J., & Harper, D. (2003). *Animal signals*, Oxford University Press.

Meyhöfer, R., Casas, J., & Dorn, S. (1997). Vibration–mediated interactions in a host–parasitoid system. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264(1379), 261-266. https://doi.org/10.1098/rspb.1997.0037

Miyatake, T., Matsumura, K., Kitayama, R., Otsuki, K., Yuhao, J., Fujisawa, R., & Nagaya, N. (2019). Arousal from tonic immobility by vibration stimulus. *Behavior Genetics*, 49(5), 478-483. https://doi.org/10.1007/s10519-019-09962-x

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS Medicine*, 6(7), e1000097. https://doi.org/10.1371/journal.pmed.1000097

Moore, T. E. (1961). Audiospectrographic analysis of sounds of Hemiptera and Homoptera. *Annals of the Entomological Society of America*, 54(2), 273-291. https://doi.org/10.1093/aesa/54.2.273

Mukai, H., Hironaka, M., Tojo, S., & Nomakuchi, S. (2014). Maternal vibration: an important cue for embryo hatching in a subsocial shield bug. *PLoS One*, 9(1), e87932. https://doi.org/10.1371/journal.pone.0087932

Muraoka, T., Onoye, H., & Takayanagi, A. (1974). Measurement of phonograph cartridges by the pulse-train method. *Journal of the Audio Engineering Society*, 22(7), 502-510.

Nishide, Y., & Tanaka, S. (2016). Desert locust, *Schistocerca gregaria*, eggs hatch in synchrony in a mass but not when separated. *Behavioral Ecology and Sociobiology*, 70(9), 1507-1515. https://doi.org/10.1007/s00265-016-2159-2

Njoroge, A. W., Affognon, H., Mutungi, C., Rohde, B., Richter, U., Hensel, O., & Mankin, R. W. (2016). Frequency and time pattern differences in acoustic signals produced by *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) and *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) in stored maize. *Journal of Stored Products Research*, 69, 31-40. https://doi.org/10.1016/j.jspr.2016.06.005

Ossiannilsson, F. (1949). Insect drummers. A study on the morphology and function of the sound producing organ of the Swedish Homoptera Auchenorrhyncha with notes on their sound production. *Opuscula Entomologia*. 1949, 10, 1–146.

Pearman, J. V. (1928). On sound production in the Psocoptera and on a presumed stridulatory organ. *Entomologists Monthly Magazine*, 64(14), 179-186.

Pfannenstiel, R. S., Hunt, R. E., & Yeargan, K. V. (1995). Orientation of a hemipteran predator to vibrations produced by feeding caterpillars. *Journal of Insect Behavior*, 8(1), 1-9. https://doi.org/10.1007/BF01990965

Polajnar, J., Eriksson, A., Lucchi, A., Anfora, G., Virant-Doberlet, M., & Mazzoni, V. (2015). Manipulating behaviour with substrate-borne vibrations–potential for insect pest control. *Pest Management Science*, 71(1), 15-23. https://doi.org/10.1002/ps.3848

Puranik, P. G., Ahmed, A., & Siddiqui, M. A. (1981). The mechanism of sound production in the pentatomid bug *Tesseratoma javanica* Thunberg. *Proceedings: Animal Sciences*, 90(2), 173-186. https://doi.org/10.1007/BF03185992

Quiroga, N., Muñoz, M. I., Pérez-Espinoza, S. A., Penna, M., & Botto-Mahan, C. (2019). Stridulation in the wild kissing bug *Mepraia spinolai*: description of the stridulatory organ and vibratory disturbance signal. *Bioacoustics*, 29(3), 266-279. https://doi.org/10.1080/09524622.2019.1603120

R Development Core Team (2020). R: A Language and Environment for Statistical Computing. http://www.R-project.org

Rajendran, S. (1999). Detection of insect infestation in stored food commodities. *Journal of Food Science and Technology* 1999, 36, 283–300

Rosengaus, R. B., Jordan, C., Lefebvre, M. L., & Traniello, J. F. A. (1999). Pathogen alarm behavior in a termite: a new form of communication in social insects. *Naturwissenschaften*, 86(11), 544-548. https://doi.org/10.1007/s001140050672

Rosi-Denadai, C. A., Araújo, P. C. S., Campos, L. A. D. O., Cosme Jr, L., & Guedes, R. N. C. (2020). Buzz-pollination in Neotropical bees: genus-dependent frequencies and lack of optimal frequency for pollen release. *Insect Science*, 27(1), 133-142. https://doi.org/10.1111/1744-7917.12602

Schneider, S. S., & Lewis, L. A. (2004). The vibration signal, modulatory communication and the organization of labor in honey bees, *Apis mellifera*. *Apidologie*, 35(2), 117–131. https://doi.org/10.1051/apido:2004006

Schwarzer, G., Carpenter, J. R., & Rücker, G. (2015). *Meta-analysis with R*. Springer. https://doi.org/10.1007/978-3-319-21416-0

Scott, J. L., Matheson, S. M., & Yack, J. E. (2010). Variation on a theme: Vibrational signaling in caterpillars of the rose hook-tip moth, *Oreta rosea*. *Journal of Insect Science*, 10(1), 1-15. https://doi.org/10.1673/031.010.5401

Scott, J. L., & Yack, J. E. (2012). Vibratory territorial signals in caterpillars of the poplar lutestring, *Tethea or* (Lepidoptera: Drepanidae). *European Journal of Entomology*, 109(3), 411–417. https://doi.org/10.14411/eje.2012.053

Stewart, K. W. (1997). Vibrational communication in insects. Epitome in the language of stoneflies? *American Entomologist,* 43, 81–91. https://doi.org/10.1093/ae/43.2.81

Strübing, H. (1958). Lautäuβerung – der entscheidende Faktor für das Zusammenfinden der Geschlechter bei Kleinzikaden (Homoptera – Auchenorrhyncha) (Vorläufige Mitteilung). *Zoologische Beiträge*. 4(1), 15–21.

Suryanarayanan, S., & Jeanne, R. L. (2008). Antennal drumming, trophallaxis, and colony development in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Ethology*, 114(12), 1201-1209. https://doi.org/10.1111/j.1439-0310.2008.01561.x

Suryanarayanan, S., Hermanson, J. C., & Jeanne, R. L. (2011). A mechanical signal biases caste development in a social wasp. *Current Biology*, 21(3), 231-235. https://doi.org/10.1016/j.cub.2011.01.003

Takanashi, T., Fukaya, M., Nakamuta, K., Skals, N., & Nishino, H. (2016). Substrate vibrations mediate behavioral responses via femoral chordotonal organs in a cerambycid beetle. *Zoological Letters*, 2(1), 1-7. https://doi.org/10.1186/s40851-016-0053-4

Takanashi, T., Uechi, N., & Tatsuta, H. (2019). Vibrations in hemipteran and coleopteran insects: behaviors and application in pest management. *Applied Entomology and Zoology*, 54(1), 21-29. https://doi.org/10.1007/s13355-018-00603-z

Tautz, J., Roces, F., & Hölldobler, B. (1995). Use of a sound-based vibratome by leaf-cutting ants. *Science*, 267(5194), 84-87. https://doi.org/10.1126/science.267.5194.84

Tschuch, G., & Brothers, D. J. (1999). Modeling vibration and sound production in insects with nonresonant stridulatory organs. *The Journal of the Acoustical Society of America*, 106(6), 3706-3710. https://doi.org/10.1121/1.428227

Uman, L. S. (2011). Systematic reviews and meta-analyses. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, 20(1), 57-59.

Virant-Doberlet, M., & Čokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33(2), 121-134. https://doi.org/10.1590/s1519-566x2004000200001

Virant-Doberlet, M., Kuhelj, A., Polajnar, J., & Šturm, R. (2019). Predator-prey interactions and eavesdropping in vibrational communication networks. *Frontiers in Ecology and Evolution*, 7, 203. https://doi.org/10.3389/fevo.2019.00203

Watanabe, K. (1978). Phonograph for use with record cartridges. U.S. Patent No. 4,123,065. Washington, DC: U.S. Patent and Trademark Office.

Yack, J. E., Smith, M. L., & Weatherhead, P. J. (2001). Caterpillar talk: acoustically mediated territoriality in larval Lepidoptera. *Proceedings of the National Academy of Sciences*, 98(20), 11371-11375. https://doi.org/10.1073/pnas.191378898

Yack, J. E., Gill, S., Drummond-Main, C., & Sherratt, T. N. (2014). Residency duration and shelter quality influence vibratory signalling displays in a territorial caterpillar. *Ethology*, 120(4), 354-364. https://doi.org/10.1111/eth.12210

Yack, J. E. (2016). Vibrational signaling. In G. S. Pollack, A. C. Mason, A. N. Popper, R. R. Fay (Eds.), *Insect hearing* (pp. 99–123). Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-28890-1_5

Yadav, C., Guedes, R. N. C., Matheson, S. M., Timbers, T. A., & Yack, J. E. (2017). Invitation by vibration: recruitment to feeding shelters in social caterpillars. *Behavioral Ecology and Sociobiology*, 71(3), 51. https://doi.org/10.1007/s00265-017-2280-x

CHAPTER 2

What's shaking for caterpillars? Leaf-borne vibratory stimuli and behavioral responses in the fall armyworm, *Spodoptera frugiperda*

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Abstract

Caterpillars are substrate-bound insects that exhibit highly varied and sometimes complex behaviors that require interacting with their environments. Leaf-borne vibrations are predicted to be crucial to caterpillars for communication and risk assessment. Yet, little is known about the vibratory landscape of caterpillars. To address this, we used the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), as a model. There were two main goals of this study: first, using a laser-doppler vibrometer, to record and characterize the vibratory landscape on a leaf in the presence of abiotic (wind and raindrops) and biotic (caterpillars and predatory stinkbug) stimuli, and second, to assess whether different larval instars detect and respond to these vibrations. The results show that vibrations from abiotic and biotic stimuli were distinct from background noise (i.e., without stimulus), except those produced by the crawling of 1st instar larvae. The spatial analysis revealed that abiotic vibration characteristics were more widely spread across the leaves. Wind-induced leaf movement produced vibrations with a low-frequency (99.7 Hz) and high-amplitude (2.97 $mm.s^{-1}$), whereas raindrops generated higher frequency (174 Hz) and higher amplitude vibrations (3.25 $mm.s^{-1}$). In contrast, vibrations produced by fall armyworm crawling or stinkbug walking on leaves was less uniformly distribution, concentrating on some leaf regions. The crawling of 1st instar larvae did not produce noticeable vibrations (63.4 Hz and 0.65 $mm.s^{-1}$), but vibrations produced by 2nd to 5th instars were distinct from background levels with dominant frequencies ranging from 243 to 326 Hz and amplitudes from 1.42 to 2.95 $mm.s^{-1}$. Similarly, predatory stinkbugs walking on leaves also produced noticeable vibrations with a dominant frequency of 140 Hz and amplitude of 2.92 $mm.s^{-1}$. Caterpillars exposed to wind and rain stimuli behaved differently than unexposed caterpillars, regardless of instar. Caterpillars exposed to wind responded with a greater transition from crawling to touching around, whereas caterpillars exposed to raindrops responded with a greater transition from crawling to resting. Caterpillars exposed to biotic stimuli did not exhibit a consistent response among instars. First instar caterpillars did not respond to biotic stimuli, but 2nd to 5th instars respond differently to another organism's approach. When approached by a conspecific, caterpillars spend less time feeding and more time crawling, touching around, or resting, and eventually produced defensive behaviors (e.g., mandible scraping, biting, dodging, and dropping off). Caterpillars exposed to predators, on the other hand, spent more time freezing, feeding, and resting, eventually including other defensive behaviors (e.g., mandible scraping, biting, dodging, rearing up, and jerking). The results contribute novel insights into a caterpillar's vibroscape and further demonstrate how the fall armyworm can detect and respond to vibrations for its survival. This fills a gap in our understanding of the sensory ecology of this economically important pest species.

Keywords: caterpillar, predatory stinkbug, spatial distribution; biotremology, vibrational communication.

Introduction

Vibratory sensing and communication in insects is widespread and has received significant attention in recent decades. There is a burgeoning body of evidence for the importance of solid-borne vibrations in a variety of behaviors, ranging from the detection of passive cues to complex communication signals (Virant-Doberlet & Čokl 2004; Cocroft & Rodríguez 2005; Cocroft et al. 2014; Hill et al. 2019). Despite the rapid progress of this field, a research bias remains in favor of adults, leaving a significant knowledge gap on the role of vibration for juveniles

(Turchen et al. [In press]). Caterpillars, for instance, are obligate substrate-bound insects that face the daunting task of coping with a complex environment that includes biotic and abiotic noise, as well as interactions with competitors and exploiters. The ability to detect and distinguish plant-borne vibrations arguably plays a crucial role in their sensory ecology and survival (Yack 2016; Yack & Yadav [In press]). There is a growing body of literature demonstrating or suggesting that caterpillars are capable of detecting and discriminating between vibration sources in a variety of contexts, including predator detection and risk assessment (Bacher et al. 1996; 1997; Castellanos & Barbosa 2006), detection of abiotic events such as wind and rain (Guedes et al. 2012), recruitment and spacing (Fletcher et al. 2006; Yadav et al. 2017), territorial defense (Yack et al. 2001; 2014; Bowen et al. 2008), and maintaining relationships with ants (De-Vries 1990; Travassos & Pierce 2000; Lin et al. 2019; Casacci et al. 2019). Even so, the natural vibratory landscapes of caterpillars living on different plant substrates, and who are exposed to a range of different biotic and abiotic factors, remains poorly understood for most species. In this study, we studied the vibratory environment of caterpillars, using the fall armyworm as a model.

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera: Noctuidae), originated from the Americas but has become an invasive pest in Africa (in 2016), Asia (in 2018), and Oceania (in 2020) recently (Deshmukh et al. 2021; Wan et al. 2021). This species is a highly polyphagous pest and is reported to attack over 350 commercial and non-commercial hosts across 76 plant families, including mainly Poaceae, Asteraceae, and Fabaceae (Montezano et al. 2018). Understanding the sensory ecology of a pest species is critical for generally understanding its life history, and for development of control measures. While the acoustic sensory ecology of adult fall armyworms has received some research attention (e.g., Tougaard 1998; Nakano et al. 2009; 2010; Mora et al. 2014), to the best of our knowledge, the vibrations generated or received by fall armyworm larvae have not been studied.

Solid-borne vibrations that caterpillars might encounter in their environment is predicted to be abundant and complex. The vibratory landscape of any organism is a collection of biological, geophysical, and anthropogenic vibrations emanating from a given landscape to create unique vibrational patterns across a variety of spatial and temporal scales (Šturm et al. 2019). For caterpillars that live on plants, for instance, the main source of biotic vibrations is emitted by arthropods, not only during intraspecific communication, but also as a by-product of other activities (e.g., incidental vibrations induced during walking, feeding, or grooming) (Yack 2016; Yack & Yadav [In press]). Additionally, caterpillars are exposed to vibrations from abiotic sources, which can be produced in plants when the wind induces oscillations in leaves or stems; or when raindrops strike the leaf surface (Casas et al. 1998). Both biotic and abiotic vibratory sources potentially provide a wealth of information that can be used by a multitude of potential receivers within a vibrational communication network (as proposed by Virant-Doberlet et al. 2019). However, it is noteworthy that the richness and complexity of this vibratory world are not attributable only to vibration sources but also to the medium through which the vibrations travel. Plants, for instance, are highly complex structures and exhibit wide variability in traits that might act as a physical constraint on the mechanical wave and can affect the transmission and perception of vibratory stimuli (Michelsen et al. 1982; Cocroft et al. 2006; Joyce et al. 2014; Velilla et al. 2020). It may lead to relevant consequences for organisms living on plants, such as caterpillars, by limiting the area over which they can gather or send vibrational information (i.e., vibratory active space, Mazzoni et al. 2014). Therefore, a comprehensive characterization of the sensory environment is crucial for understanding what vibrations are available to an organism, and how vibration is scattered through the substrate and its potential to trigger a behavioral response of organisms within a landscape.

This study had two primary goals. The first was to record and characterize the vibroacoustic landscape on a leaf scale in the presence of different abiotic (wind and raindrops) and biotic (caterpillars and predatory stinkbug) stimuli. We addressed this by recording vibrations across the leaf surface and then used spatial interpolation to map the distribution of dominant frequency (Hz) and amplitude (mm s^{-1}) throughout the leaves. The second goal was to test whether larvae detect and respond to vibrations from abiotic and biotic sources, examining behavioral responses of the caterpillars in the presence of these vibrations.

Material and methods

Insect rearing and plant material

Two insect species were included in these experiments: larvae of the fall armyworm, *S. frugiperda*, and adults of the predatory stinkbug *Podisus nigrispinus* (Dallas, 1851) (Hemiptera: Pentatomidae). Both were obtained from colonies maintained under laboratory conditions at the Department of Entomology of the Federal University of Viçosa. In fall armyworm rearing, moths were maintained in PVC cages (40 cm high × 30 cm in diameter) with sulfite paper on the inner walls for oviposition; cotton soaked in a solution of 10% sugar and 5% ascorbic acid was provided as food. Eggs were collected and stored in plastic bags until hatching. Batches of neonates were transferred to an artificial diet (Kasten et al. 1978) in 500-ml plastic cups until the 2nd instar and then individually until pupation. In stinkbug rearing, the nymphs and adults were kept in cages and fed *Tenebrio molitor* Linnaeus, 1758 (Coleoptera: Tenebrionidae) pupae and leaves of *Eucalyptus grandis* (W. Hill ex. Maiden) ad libitum. All insects were kept at a controlled temperature of 27 ± 2 °C, relative humidity of 70 ± 15%, and 14L:10D photoperiod.

The plant used in experiments was green bean (*Phaseolus vulgaris* L.), which is listed as a host plant of the fall armyworm (Montezano et al. 2018). Plants were grown in pots (1.7 L) containing a mixture of soil, washed coarse sand, and organic matter, in a ratio of 1:1:1 (v/v/v), and commercial substrate in a ratio of 3:1 (v/v). Plants were housed in a greenhouse (temperature of 28±8°C, relative humidity of 65±9%, and maximum natural irradiance), free from insect infestation, and received the fertilization recommended for the crop. When they reached the phenological stage V_3-V_4 (20-25 cm of height), the plants were used in the trials.

Vibration and video recording set up

Leaf vibrations and insect behaviors were recorded simultaneously using a laser-Doppler vibrometer and camcorder. Two different recording scenarios with slightly different recording conditions were performed (see sections 2.3 and 2.4 below). Here we describe the general recording set up. Bean plants 20-25 cm tall were transported from the greenhouse to the laboratory and individually placed on top of a vibration isolating table (63-500 Series Micro-g; TMC, Peabody, MA, USA). Afterward, the leaves (attached to plants) with a size of ~8 x 10 cm were tagged to be used in trials (Fig. 1A). Prior to recording, one or more pieces of reflective tape (1x1 mm) were affixed to the upper surface of the leaf (Fig. 1B, C). The laser vibrometer (PVD-100; Polytec, Waldbronn, Germany) was set with a velocity of 100 mm. s^{-1} (or 25 mm. s^{-1}/V), high-pass filter off, and low-pass filter set at 20 kHz. The laser beam was positioned perpendicularly to the reflective tape. The analog output of the laser vibrometer was connected to an oscilloscope (TDS-2012C; Tektronix, Beaverton, OR, USA) to measure instantaneous voltages directly from the laser. These voltages were used to calculate instantaneous velocity. Simultaneously, the digital output of the laser vibrometer was connected to the microphone port of a high-resolution camcorder (HDR-CX455; Sony, Tokyo, Japan) to sync audio-video recordings. The camcorder was set for 1920×1080 pixels with 30 frames/second and an audio sampling rate of 48 kHz with 16-bit resolution. All the recordings were performed on top of the vibration isolating table to reduce external interference (see Fig. 1A).

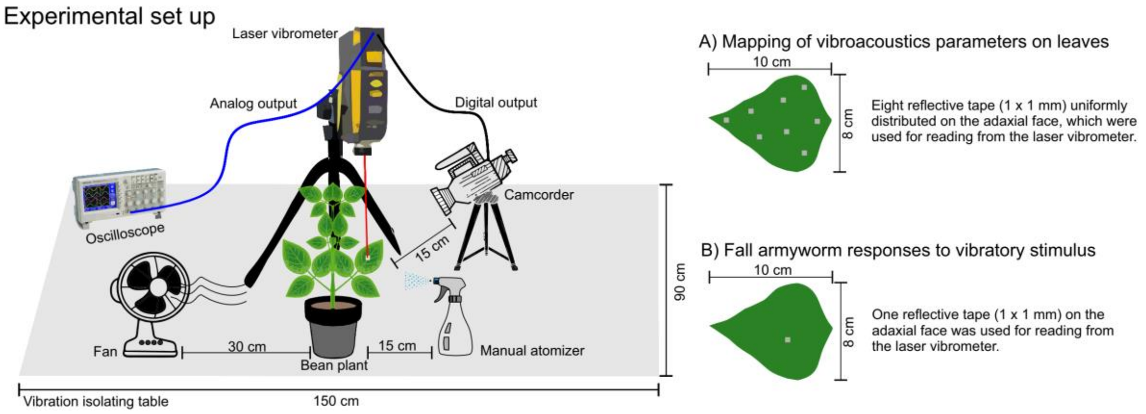

Fig. 1. Schematic illustrations of the experimental set-up (A) and recording scenarios used for mapping of vibroacoustic parameters on leaves (B) and fall armyworm response to vibratory stimulus (C).

Audio files were extracted from videos (waveform audio, '.wav') using software Audacity(R) [version 3.0.2] with the FFmpeg library (Audacity Team, 2021). Audio files were analyzed for the characterization of dominant frequency (Hz) and amplitude (mm.s-1). Peak frequency was taken from the spectrum (sampling frequency: 22.050, window type: "Hanning," window size: 1,024, overlap: 50), which were performed using the R packages 'tuner', 'seewave', and 'phonTools', according to procedures described by Sueur (2018). The amplitude in audio was corrected based on instantaneous velocity obtained from the analog output of the laser vibrometer. The video files (mega tree session, '.mts') with the behavioral responses of fall armyworms were analyzed using the BORIS behavior analysis software (Friard & Gamba, 2016). A list containing the brief behavioral descriptions (Table S1) was used as a reference during behavioral annotation. See details below on specifics of audio and video sampling and analysis.

Mapping of vibroacoustic parameters on leaves

The goal of this experiment was to characterize the vibroacoustic characteristics of bean leaves and to describe how vibrations are spatially distributed in the presence of different abiotic and biotic stimuli. In this bioassay, eight pieces of reflective tape (1x1 mm) were uniformly distributed on the adaxial face of a pre-selected bean leaf for recording with the laser vibrometer (Fig. 1B). Subsequently, the leaf was submitted to one of the following conditions: (i) background noise (i.e., control) - that was recorded in the absence of external vibration provided to plants. (ii) vibration produced by abiotic factors - that consisted of a simulation of light wind or moderate rain. The wind was simulated using a domestic fan (Arno S.A., Brazil) at a velocity of 1.3 m/s (measured with a Knup Anemometer, KP-8016) positioned at a distance of 30 cm from a bean plant. The fan was turned on for approximately 30s at a rate of 1 event per minute

(Fig. 1A). Raindrops were simulated using a manual atomizer sprayed from a distance of 15 cm from the bean leaf, delivering multiple and simultaneous water droplets to the leaf surface at a rate of about two spritzes per minute and a volume of 0.15 ml per spritz (Fig. 1A). (iii) vibration from biotic factors - a larva *S. frugiperda* (from first to fifth instar) or an adult predatory stinkbug released individually on the central region of the leaf and recording the vibrations produced by caterpillar crawling or stinkbug walking on the substrate (Fig. 1A). Leaf vibrations resulting from each stimulus were recorded with a laser and video simultaneously, as described in section 2.2. Herein, recordings were performed on each reflective tape (i.e., sampling point) individually for 120 s. This procedure was recorded in triplicate (i.e., 3 leaves with 8 points) for each condition. After each replicate, the leaf and insect (when used) were replaced. The audio and video files were analyzed using BORIS to identify the segments containing a stimulus (i.e., wind, raindrops, caterpillar crawling, and stinkbugs walking). For each sampling point, three recording segments (windows of 30 s per segment) containing the stimulus were used for temporal, spectral, and amplitude characterization of the vibration, totaling 24 segments in each replicate. The average of dominant frequency (Hz) and amplitude (mm s^{-1}) obtained in each sample point were used for the overall characterization of vibration and building of spatial models. See details below on statistical analysis.

Fall armyworm responses to vibratory stimulus

The goal of this experiment was to assess whether larvae of each instar responded to vibrations from abiotic and biotic sources. In this bioassay, a bean plant with leaves previously tagged was placed on a vibration isolating table. One piece of reflective tape (1x1 mm) attached to the central region of the adaxial face of the leaf was used for reading from the laser vibrometer (Fig 1C). For each replicate, a caterpillar was collected from a cup with diet and placed on a pre-selected bean leaf. The caterpillar was left undisturbed for at least 2 minutes on the isolated leaf to allow for acclimatization before commencing the recording session. Following acclimatization, leaf vibrations and larval behaviors were recorded while a caterpillar was submitted to one of following trials: (i) background noise (i.e., control) (no-stimulus on leaf) [n=10 replicates/instars]; (ii) simulated wind [n=10 replicates/instar]; (iii) raindrops [10 replicates/instar]; (iv) approaching by conspecific of the same instar [n=10 replicates/instar] or (v) approaching by an adult of a predatory stinkbug [n=10 replicates/instar].

All stimuli were tested separately, and the caterpillar was replaced in each replicate. In the trials where a caterpillar was exposed to background noise (or control), wind, or raindrops, the simulation of abiotic factors occurred under the same conditions described above except that only a single reflective disc was attached to the leaf for recording. In trials where a caterpillar was exposed to a conspecific of the same instar or a predator, the recordings started 1 min prior to introducing the other organism with a paintbrush to the leaf. In trials with predators, the stinkbugs were individually held in a plastic vial and food-deprived for at least 12 h prior to the trial. In all trials, the interactions were recorded for 10 min or until an organism left the leaf or the predator attacked the caterpillar. In this bioassay, the audio and video files were entirely analyzed using BORIS to assess the behavioral responses of fall armyworms and the frequency of behavioral transitions when exposed to different stimuli. Table S1 summarizes the categories used to classify behaviors in video records. We specifically focused on the behavioral response of the first caterpillar on the leaf (i.e., resident, focal animal) because we were interested in assessing their response to the stimulus provided. The results were represented as simplified ethograms based on first-order behavioral transitions after exposure to each stimulus.

Statistical analyses

All analyses were performed using the R-software [version 4.0.1] run in the RStudio interface [version 1.4.1] (R Core Team 2021; RStudio Team, 2021). The graphical illustrations were produced with Wacom creative table (Intuos S, Tokyo, Japan) using Corel Painter (Essential 7, Ottawa, ON, Canada).

Vibroacoustic parameters

To characterize the vibroacoustic parameters of bean leaves and verify whether they differ from background noise, the data from dominant frequency (Hz) and amplitude (mm. s^{-1}) were subjected to analyses of deviance and generalized linear model (GLM) with *Gaussian* distribution. Subsequently, the assumptions of normality and homoscedasticity of model residuals were checked with Shapiro-Wilk and Bartlett tests, respectively. When required, the overdispersion of models was adjusted and significant treatments were compared by the test of contrasts ($P < 0.05$), using the R package “stats”.

Spatial analysis and mapping of vibroacoustic parameters

To assess how vibrations are spatially distributed across the leaf in the presence of different abiotic and biotic stimuli, suitable spatial models were selected and tested based on the distances between the leaf sampling points; the averages of dominant frequency (Hz) and amplitude ($mm.s^{-1}$) were determined for each sampling point with a laser vibrometer. The empirical semivariogram (i.e., the variance of variable differences between two sampling points) was used to adjust the best model to fit the theoretical semivariogram as a function of the spatial location of the determinations. The semivariogram models tested were spherical, exponential, and Gaussian. The models were selected using cross-validation with the best data adjustment using the R package ‘performance’. The semivariogram functions allowed for the estimation of three parameters: range (r), partial sill (C), and nugget (C_0) (Isaaks & Srivastava, 1989). The first parameter, range (r), indicates the distance of spatial autocorrelation. The second parameter refers to its respective semivariance value, which increases and then reaches the sill ($C_0 + C$). The third, nugget (C_0), refers to the intercept of the y-axis on the semivariogram and represents variance occurred at scales finer than lag distance. Two further parameters were determined from the basic parameters described above: the sill ($C_0 + C$) and level of spatial dependence (LSD) [$C_0/ (C_0 + C)$], where the spatial dependence of the semivariogram is considered strong when $LSD \leq 0.25$, moderate when $0.25 < LSD < 0.75$ and weak when $LSD > 0.75$ (Cambardella et al., 1994). The spatial maps depicting the vibroacoustic distribution on leaves were generated using the semivariance data obtained with the selected models, according to procedures described by Brunsdon & Comber (2019) using the R packages “sf”, “stars”, “gstat”, “geoR”, “rgdal” and all dependent.

Behavioral analysis

The behavioral responses of fall armyworms were represented as simplified ethograms based on first-order behavioral transitions after each stimulus. To test whether the behavioral transitions of the fall armyworm were independent of the vibratory stimulus, the frequencies of the behavioral transitions of caterpillars in the control [without stimulus] were contrasted with the behavioral transition of caterpillars exposed to each vibratory stimulus using the G–test of independence in contingency tables and the measure of association between variables was estimated using Cramer's V, with the R package “DescTools”. Cramer's V values range of 0 - 0.3 is considered as weak, 0.3 - 0.7 as medium, and > 0.7 as strong. The proportion of time spent in each behavior was submitted to the Kruskal-Wallis test by ranks (H-test) when significative post-hoc tests were performed using Fisher's least significant difference (LSD) test ($P < 0.05$) with the R package “agricolae”.

Results

Characteristics of leaf vibrations and mapping of vibroacoustic parameters

Leaf vibrations resulting from exposure to abiotic and biotic factors differed in the dominant frequency ($F_{8,207}$= 50.10; $P < 0.01$; Fig.2A) and amplitude ($F_{8,207}$= 33.63; $P < 0.01$; Fig.2B). Overall, vibrations from abiotic and biotic stimuli were distinct from background noise, except for those produced by crawling of 1st instar larvae which exhibited dominant frequency and amplitude similar to background noise (i.e., vibrations were almost undetectable by the laser). By contrast, simulated wind and raindrops, crawling of 2nd to 5th instar larvae, and walking of predatory stinkbugs exhibited dominant frequencies ranging from 100-350 Hz and amplitudes > 1 $mm.s^{-1}$ (Fig 2).

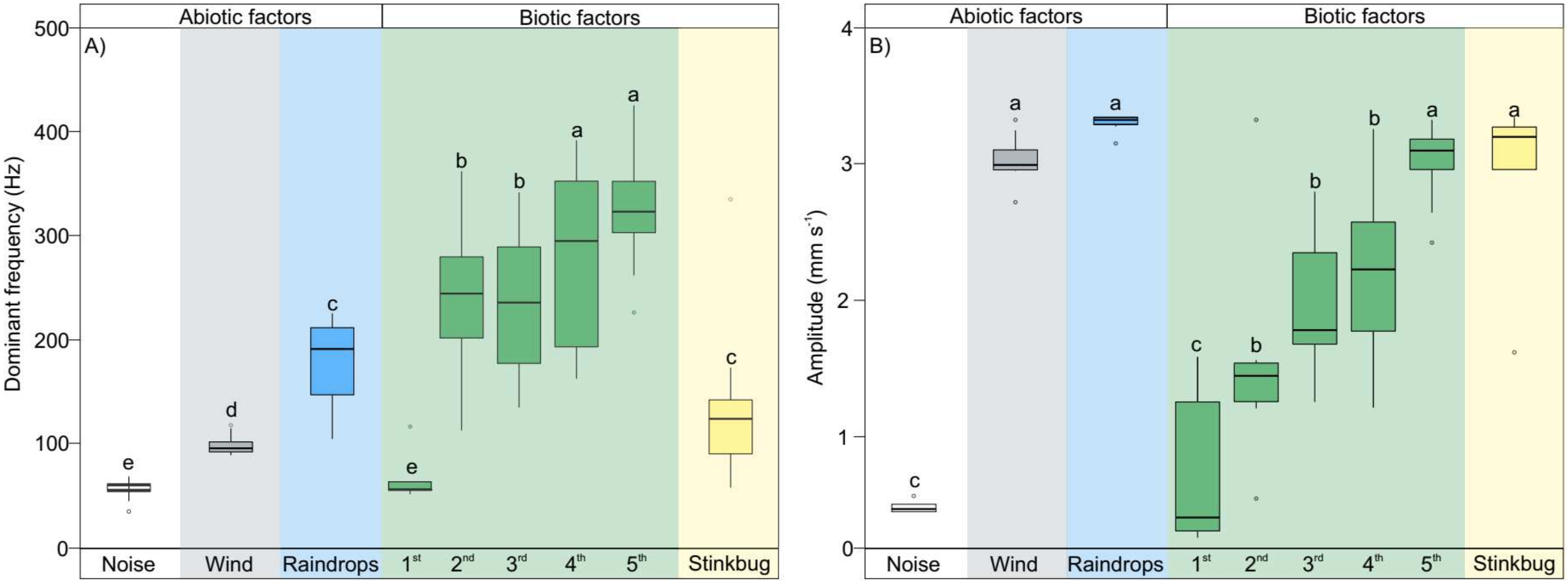

Fig. 2. Dominant frequency (A) and amplitude (B) of leaf vibrations when exposed to background noise – no stimulus (empty boxplot), wind (gray boxplot), raindrops (blue boxplot), crawling of fall armyworm from 1st to 5th instar (green boxplot), and walking of predatory stinkbug (yellow boxplot). Box plots indicate the median (solid line) and dispersal (lower and upper quartiles and outliers) of the vibroacoustic parameters. Different letters at the top of the box plot indicate significant differences by contrast test ($P < 0.05$).

Based on “Tobler’s First Law of Geography”, which states that things close together are more similar than things farther apart, we used spatial interpolation with the purpose to map the distribution of dominant frequency (Hz) and amplitude (mm. s^{-1}) through bean leaves (Fig. 3), while recording these traits at spatially distributed sampling points spread over the leaf surface. Regardless of the stimulus, the semivariogram models showed similar spatial autocorrelation (range = 2.47 cm) and strong spatial dependency (LSD ≤ 0.11), suggesting that vibroacoustic parameters were not randomly distributed on the leaves (Table S2). Indeed, the vibroacoustic parameters were more uniformly distributed through leaves when submitted to background noise (Fig. 3A), wind (Fig. 3B), and raindrops (Fig. 3C), although there is a clear difference in levels of dominant frequency and amplitude when compared between each stimulus (see Fig. 2). By contrast, the vibrations produced by armyworm crawling (Fig. 3D-H) or stinkbug walking on leaves (Fig. 3I) exhibited a less uniform distribution of both vibroacoustic parameters on the leaves. In these cases, vibrations concentrate in some leaf regions, which likely relates to the position of organisms. In larvae, the variation was less evident in early instars [1st and 2nd instar, Fig. 3D-E], mainly concerning dominant frequency. On the other hand, it was more pronounced in later instars [3rd until 5th instars, Fig. 3F-H], regardless of vibratory parameters.

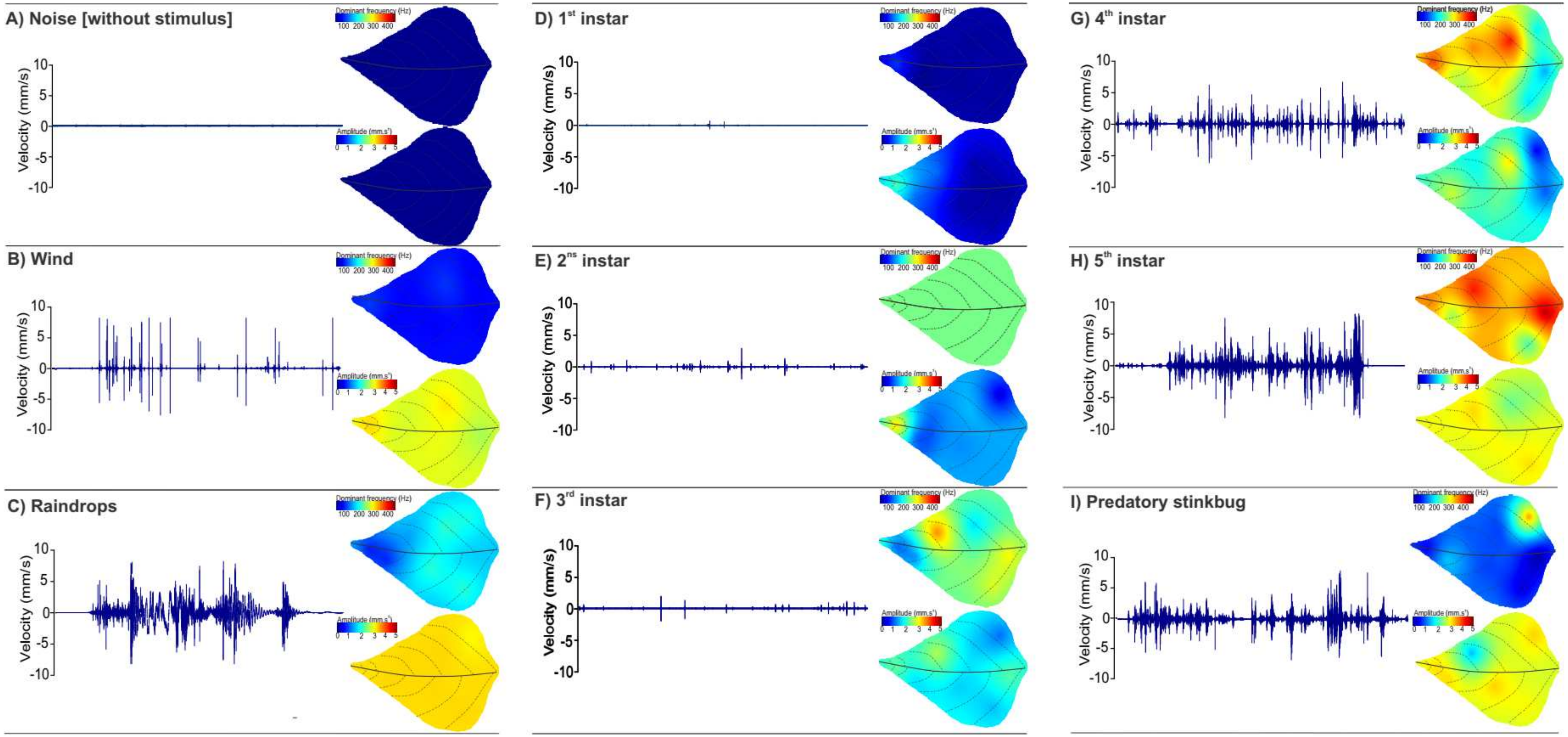

Fig. 3. Waveforms and spatial distribution of dominant frequency [top-right leaf of each section] and amplitude [bottom-right leaf of each section] produced through the bean leaf when submitted to background noise (A), wind (B) raindrops (C), the fall armyworm of 1st instar crawling (D), 2nd instar crawling (E), 3rd instar crawling (F), 4th instar crawling (G), 5th instar crawling (H) and solitary predatory stinkbug walking (I).

Fall armyworm responses to vibratory stimulus on the leaves

To test whether vibrations of abiotic and biotic resources might elicit behavioral responses by the fall armyworm, we subjected 1st to 5th instar larvae to each stimulus described above, and assessed their behavioral response and time spent in each behavior. Time and behavioral responses of larvae exposed to background noise (i.e., no stimuli) were used as the control, as no stimulus was provided to larvae (see Fig. S1A for details by instar).

Abiotic factors (wind and raindrops)

The behavioral responses of fall armyworm did not differ between instar when caterpillars were subjected to wind (G-test, $\chi^2 = 63,41$; d.f. = 56; $P = 0.231$) and raindrops (G-test, $\chi^2 = 74,34$; d.f. = 72; $P = 0.402$), suggesting that the behavioral response is independent of caterpillar instar. Thus, we combined the results from all instars to assess the overall response of caterpillars. Nonetheless, it is noteworthy that larvae of all instars [1st to 5th instar] exhibited different behavioral responses to wind (Fig. S1B) and raindrops (Fig. S1C) when compared with their control (Fig. S1A). Therefore, we provide supplementary materials with details of behavioral responses of each instar (Fig. S1 A-C), as well as the time budget spent on each behavior (Fig S2 A-E).

Regardless of instar, the overall response of fall armyworm when submitted to wind (G-test, $\chi^2 = 98.07$; d.f. = 14; $P < 0.001$, Fig. 4B) and raindrops (G-test, $\chi^2 = 80.08$; d.f. = 18; $P < 0.001$, Fig.4C) differed from the control condition (Fig. 4A), suggesting that larvae can detect and respond to abiotic stimuli (Fig 4). Remarkable differences in behavioral transitions were observed when wind-exposed caterpillars were compared with control-exposed caterpillars, mainly in the transition between crawling to touching around, whose frequency was much higher in wind-exposed caterpillars. Caterpillars exposed to raindrops exhibited a similar transition between crawling to touching around (Fig. 4C) when compared to control. However, there was an increase in transition between crawling to resting (Fig. 4C). In both cases, behaviors not reported in the control were incorporated into the caterpillar behavioral repertoire (e.g., wind [mandible scrape, and dropping off (Fig. 4B)]; raindrops [rearing up and jerking, dropping off, and dodging (Fig. 4C)]); however, these behaviors were less frequent.

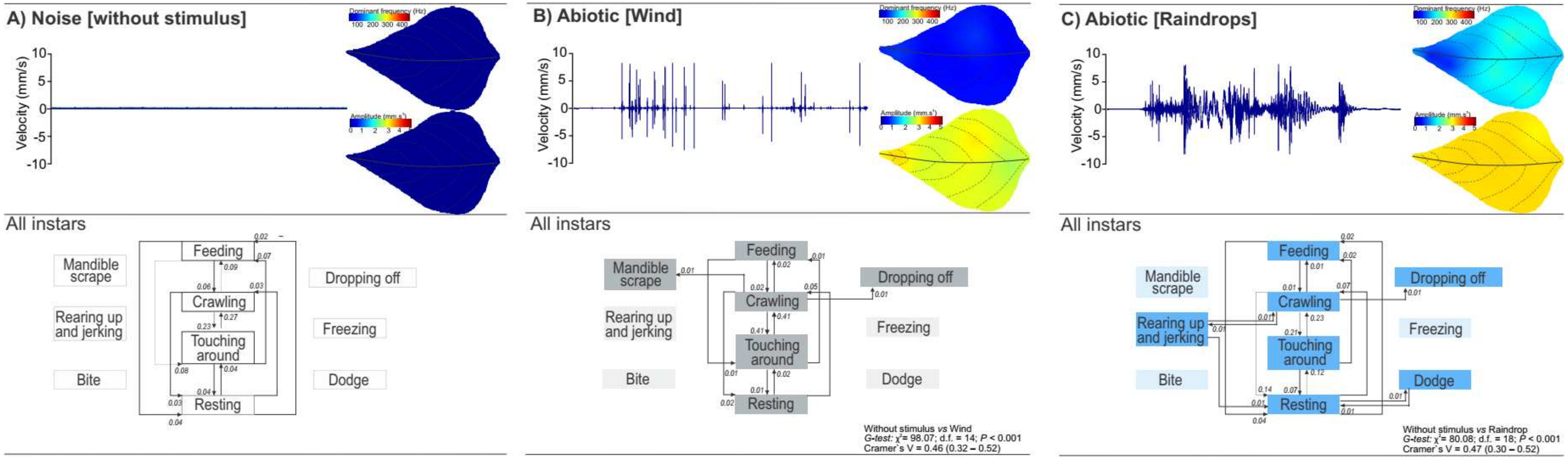

Fig. 4. Top panel shows waveforms and spatial distribution of dominant frequency (Hz) [top-right leaves] and amplitude (mm.s-1) [bottom-right leaves] through the bean leaf when exposed to background noise (A), wind (B), and raindrops (C). Bottom panel presents ethograms for each stimulus for the combined response of 1st to 5th instar larvae to these stimuli (or lack thereof). Ethograms are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark color boxes indicate the observed behaviors, while light color boxes refer to non-observed behaviors. Statistics values refer to the G–test of independence and Cramer's V.

Consistently, we observed that caterpillars subjected to background noise (i.e., control – no stimulus) did not exhibit significant differences in the proportion of time spent among behaviors (Kruskal-Wallis, $\chi^2 = 6.41$; d.f. = 3; $P = 0.09$) with a similar proportion of time spent in crawling, touching around, resting, or feeding (Fig. 5A). In contrast, caterpillars exposed to wind (Kruskal-Wallis, $\chi^2 = 13.89$; d.f. = 4; $P = 0.007$) spent more time crawling and touching around, while caterpillars exposed to raindrops (Kruskal-Wallis, $\chi^2 = 14.54$; d.f. = 5; $P = 0.01$) spent more time touching around, crawling, and resting, respectively (Fig 5A).

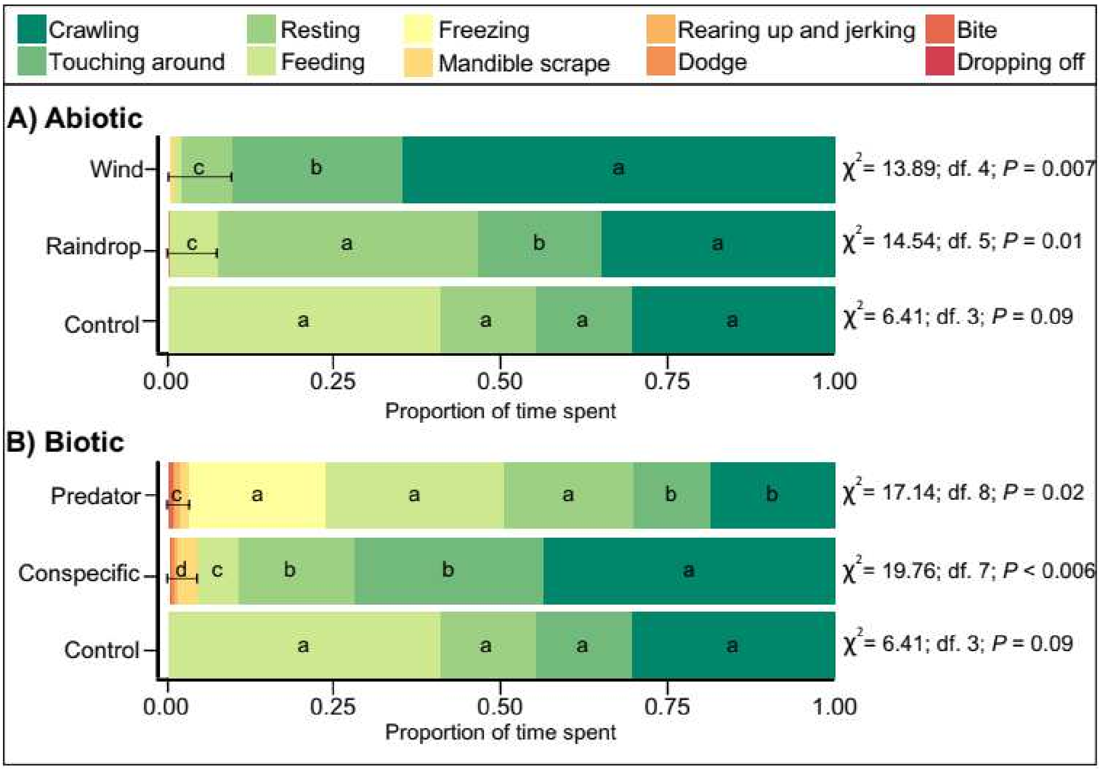

Fig. 5. Time budget spent on each behavior when caterpillars were exposed to abiotic (A) and biotic (B) stimuli. The proportion of time spent within each stimulus was submitted to Kruskal–Wallis test by ranks. Different letters within the box indicate significant differences by contrast using Fisher's least significant difference ($P < 0.05$).

Biotic factors (conspecific and predator)

The behavioral response of fall armyworms differed between instar when focal caterpillars were presented with a conspecific of the same instar (G-test, $\chi^2 = 106.06$; d.f. = 132; $P = 0.04$) or predatory stinkbugs (G-test, $\chi^2 = 215.72$; d.f. = 148; $P = 0.0002$). Therefore, the results from all instars were presented individually (Fig. 6; Fig. 7).

Behavioral responses of 1st instar caterpillars, when exposed to conspecific of the same instar, did not differ from control (G-test, $\chi^2 = 17.89$; d.f. = 10; $P = 0.056$, Fig. 6C). By contrast, the behavioral response of caterpillars of 2nd instar (G-test, $\chi^2 = 48.57$; d.f. = 15; $P < 0.001$,

Fig. 6C), 3rd instar (G-test, $\chi^2 = 35.15$; d.f. = 12; $P = 0.004$, Fig. 6C), 4th instar (G-test, $\chi^2 = 39.01$; d.f. = 21; $P = 0.010$, Fig. 6C) and, 5th instar (G-test, $\chi^2 = 92.45$; d.f. = 22; $P < 0.001$, Fig. 6C) when exposed to conspecific of the same instar differed significantly of control (Fig 6B). Second and 3rd instar(s) exhibited a higher frequency of transition between crawling to touching around (Fig. 6C). Also, in the presence of a conspecific of the same instar, the caterpillars of the 2nd and 3rd instar did not feed, and eventually showed defensive behaviors (Fig. 6C). On the other hand, caterpillars of 4th and 5th instar exhibited a higher diversity of behaviors (Fig. 6C), including non-aggressive behaviors (e.g., mandible scrape, dodge, and dropping off) and eventually aggressive behaviors (e.g., bite) (Fig 6C). Regardless of instar, caterpillars exposed to conspecific (Kruskal-Wallis, $\chi^2 = 19.76$; d.f. = 7; $P < 0.006$) spent more time crawling, touching around, or resting, with only a modest fraction of time used for feeding or defense (Fig 5). Details of the proportion of time spent in each behavior by instar are provided in the supplementary material (Fig. S3).

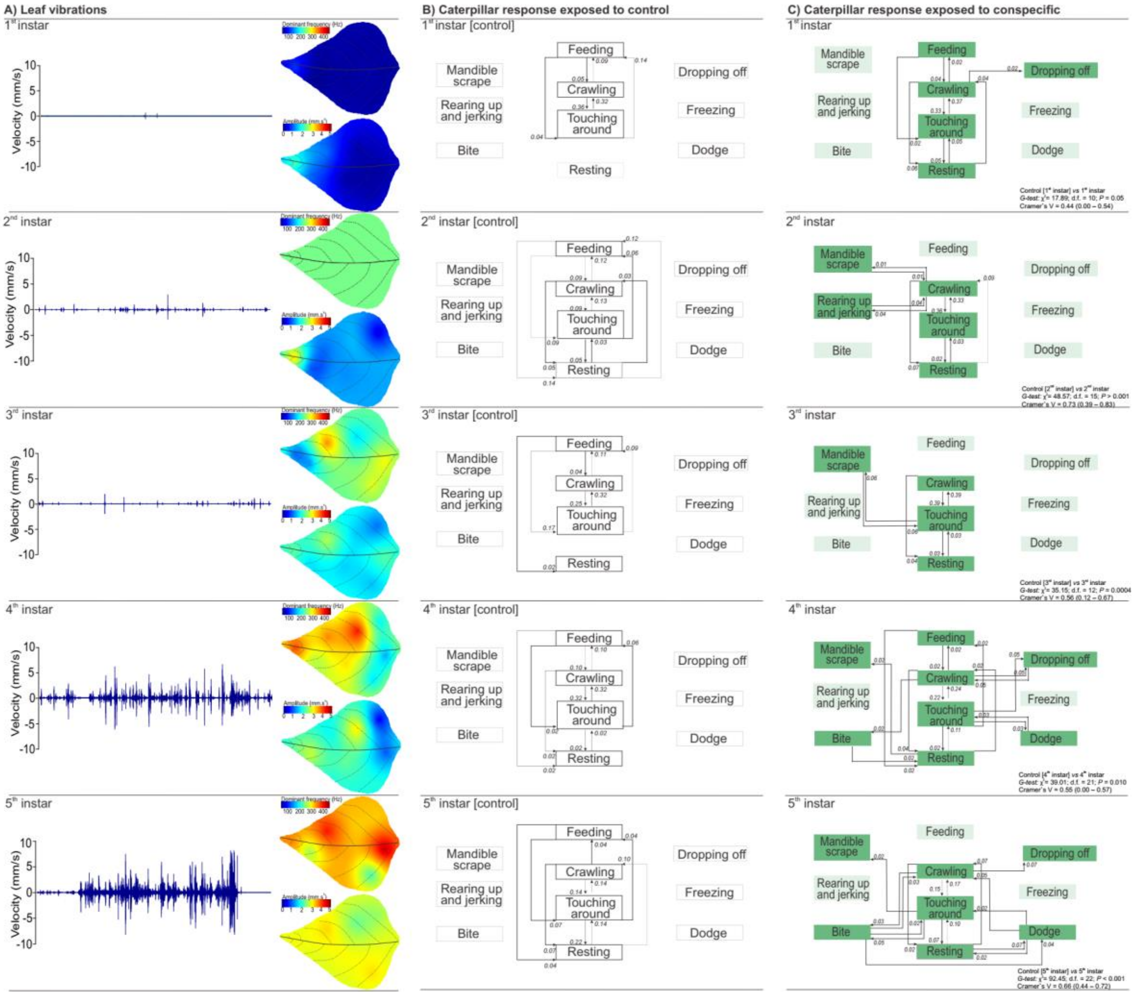

Fig 6. (A) Waveforms and spatial distribution of dominant frequency (Hz) [top-right leaves] and amplitude (mm.s^{-1}) [bottom-right leaves] represent the leaf vibrations produced by caterpillars of 1st to 5th instar. (B) Ethograms of the response of 1st until 5th when exposed to background noise (control). (C) Ethograms of the response of caterpillars of 1st to 5th instar when exposed to a conspecific of the same instar. Ethograms are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark color boxes indicating the observed behaviors, while light color boxes refer to non-observed behaviors. Statistic values refer to the G–test of independence and Cramer's V.

Similar to their behavioral response to conspecifics, 1st instar caterpillar responses to a predatory stinkbug did not differ from controls (G-test, χ^2 = 10.81; d.f. = 11; *P* = 0.459, Fig. 7A, B). By contrast, the behavioral response of 2nd instar caterpillars (G-test, χ^2 = 44.29; d.f. = 22; *P* = 0.003, Fig. 7B), 3rd instar (G-test, χ^2 = 27.01; d.f. = 14; *P* = 0.02, Fig. 7B), 4th instar (G-test, χ^2 = 36.41; d.f. = 16; *P* = 0.002, Fig. 7B) and, 5th instar (G-test, χ^2 = 182.39; d.f. = 29; *P* = 0.001, Fig. 7B) when exposed to predator differed significantly from control (Fig 7A). The presence of predators on leaves increased the repertoire of behaviors performed by caterpillars of the 2nd to 5th instar(s) (Fig. 7B). Second, 3rd, and 4th instar(s) exhibited a higher frequency of transition between crawling to touching around (see 2nd to 4th instar(s) in Fig. 7B) and eventually showed defensive behaviors. On the other hand, caterpillars from the 5th instar exhibited a higher frequency of other behaviors (Fig 7B), including aggressive (e.g., biting, rearing up, and jerking) and non-aggressive behaviors (e.g., mandible scraping, freezing, dodging, and dropping off). Regardless of instar, caterpillars exposed to predators (Kruskal-Wallis, $\chi^2 = 17.14$; d.f. = 8; $P < 0.02$) spent more time freezing, feeding, and resting, spending only a modest fraction of time used for crawling, touching around, and other behaviors (Fig 5). Details of the proportion of time spent in each behavior by instar are provided in the supplementary material (Fig. S3).

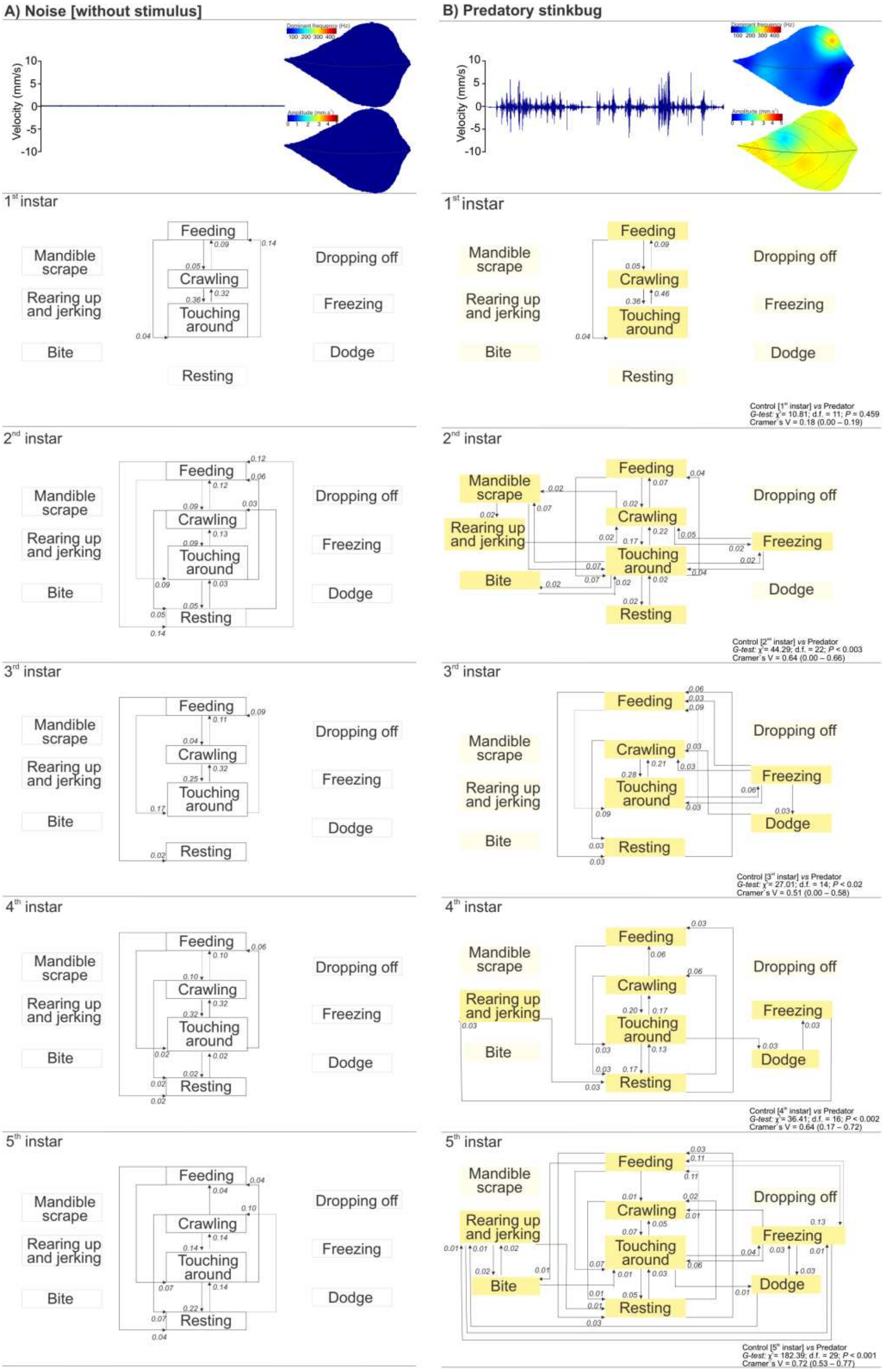

Fig. 7. Top panel shows waveforms and spatial distribution of dominant frequency (Hz) [top-right leaves] and amplitude (mm.s^{-1}) [bottom-right leaves] through the bean leaf when exposed to background noise (control) (A) and predatory stinkbug (B). Ethograms below refer to the response of caterpillars of 1st to 5th instar when exposed to each stimulus. Ethograms are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark colored boxes indicate the observed behaviors, while light colored boxes refer to non-observed behaviors. Statistic values refer to the G–test of independence and Cramer's V.

Discussion

Our perceptions shape our understanding of the world around us. Does this also apply to caterpillars? Caterpillars are substrate-bound organisms residing primarily on or within plants where vibrational information is ubiquitous and can come from a variety of sources, whether abiotic or biotic (Cocroft & Rodríguez 2005; Hill 2009). Although it is assumed that the vibratory landscape that caterpillars might encounter in their environment is complex, and that plant-borne vibrations play a crucial role in communication and risk assessment (Yack 2016; Guedes et al. 2012), the subject remains poorly understood. This study aimed to characterize vibrations of potential significance to fall armyworm caterpillars and assessed whether different instars of fall armyworms were able to detect and respond to those vibrational stimuli. We found generally that abiotic (wind and raindrops) and biotic (caterpillar and predatory stinkbug) vibrations were available to resident larvae, and that, depending on the source, they differed in their physical characteristics and distribution on the leaf. Our findings also supported the hypothesis that *S. frugiperda* larvae respond differently to vibrations produced by wind, rain, conspecifics, and predators, although we cannot rule out the possibility that other cues (e.g., visual, chemical) are involved. We discuss our findings in the context of previous studies that record the vibratory environment of caterpillars on leaves, as well as the adaptive significance of these vibrations in the context of caterpillar survival.

A leaf´s vibrant world

Our findings revealed that even on a small scale, there are complex vibratory environments. Both abiotic and biotic stimuli produced distinctive leaf vibrations, providing a vibratory landscape that potentially provides a wealth of information to assist insects in making decisions.

Vibrations induced by wind and raindrops generated a noisy environment on leaves. Wind induced a random movement of leaves, generating vibrations of low-frequency (< 100 Hz) and high-amplitude (> 3 mm.s^{-1}). Raindrops generated higher frequency (> 170 Hz) and higher amplitude (> 3 mm.s^{-1}) vibrations due to the impact of the drop on the leaf, which was followed by lower oscillations produced by their spreading out over the surface). Wind and rain are widely recognized as sources of background noise for insects that reside on plants (Cocroft & Rodríguez 2005; Hill 2009; Cocroft et al. 2014). Wind-induced vibrations are described in the literature to have generally low frequencies (< 100 Hz), albeit they may contain energy up to 20 kHz (Barth et al. 1988; Casas et al. 1998; Tishechkin 2007; McNett et al. 2010; Guedes et al. 2012). Similarly, raindrops falling on plants were reported to cause intermittent and high-amplitude waveforms with most energy below 1 kHz, which is evidently variable as it correlates to the intensity of simulated rain (Barth et al. 1988; Casas et al. 1998; Guedes et al. 2012). In our study, when leaves were exposed to abiotic stimuli, the dominant frequency and amplitude were uniformly distributed on leaves reflecting the standardized method of delivering the abiotic stimuli in our study, presumably reflecting how these stimuli would affect the leaf in nature as well. Widespread abiotic noise may impair a caterpillar's ability to perceive or distinguish relevant information, as these vibrations may overlap with those produced by conspecifics or predators, making detection or recognition of other organisms more difficult (Barth et al. 1988; Casas et al. 1998; Guedes et al. 2012). Caterpillars may also use vibrations as cues to avoid activity during rainfall or wind gusts, or, they may use episodes of environmental noise (or even the interval between them) to move (or rest) to avoid being detected, as occurs in other insects (e.g., Tishechkin 2007; Wignal et al. 2011). In these scenarios, temporal cues may be crucial for a caterpillar, but because they were not quantified, this remains speculative.

We also studied vibratory characteristics from two types of biotic sources that would be relevant to caterpillars; conspecifics of different instars, and predatory stinkbugs. Leaf vibrations produced by biotic stimuli also were distinct from the baseline, except those produced by crawling of 1st instar larvae. Vibrations caused by larval crawling on the leaf surface was predicted because the caterpillars employ two or more anchor points at the same time while moving, compressing the substrate for at least part of their crawling action (van Griethuijsen & Trimmer 2014). In contrast, stinkbugs use three legs in contact with their substrate to propel their bodies forward and provide support for the other three legs to move forward (Gullan & Crastom 2014). Although there are variations in movement, in both cases, propulsive forces are delivered to the substrate, generating oscillations in leaves as insects move, justifying our expectation. Surprisingly, the crawling of 1st instar larvae did not exhibit a noticeable oscillation on leaves. We suspect that the low frequency (< 60 Hz) and amplitude (< 1 $mm.s^{-1}$) produced by 1st instar on the leaf were insufficient to overcome the filtering propriety imposed by the substrate, making it very difficult to distinguish them. This is most likely due to the small size (< 1.7 mm) and low body weight (< 30 mg) of 1st instar caterpillars, both of which limit the ability to generate waves with sufficient energy to overcome material resistance (i.e., impedance) (Moretimer 2017). Moreover, it is reasonable to think that the sensibility of laser vibrometers was insufficient to distinguish the oscillation generated by first instar crawling from baseline noise caused by physiological processes in the plant. On the other hand, the vibrations produced by the crawling of 2nd to 5th instars exhibited a substantial vibrations on leaves with a dominant frequency ranging from 243 to 326 Hz and an amplitude ranging from 1.42 to 2.95 $mm.s^{-1}$. Predatory stinkbugs walking on leaves created notable vibrations as well, with a dominating frequency of 140 Hz and an amplitude of 2.92 $mm.s^{-1}$, which was expected due to the higher size and weight of the caterpillars, as well as the use of adult stinkbugs in the trials that increased the impact generated on the leaf surface when caterpillars crawled or stinkbugs walked. Such findings are biologically relevant in light of the fact that caterpillars may assess risk and make decisions based on unintended vibrations made by other insects, whether conspecific or predators. Also, just as caterpillars may use vibration to detect conspecifics, predators, or parasitoids, these organisms in turn may use vibration to find caterpillars (e.g., Pfannenstiel et al. 1995; Bacher et al. 1996; 1997; Meyhöfer et al. 1994; 1997; Djemai et al. 2001; 2004; Castellanos & Barbosa 2006; Virant-Doberlet et al. 2019).

Our findings indicated that, unlike abiotic stimuli, vibrations arising from biotic stimuli were concentrated in certain leaf areas, resulting in a finer mosaic of vibration and suggesting that vibrational information is only available in a limited area of the leaf. This implies in a limit to the area over which the insects can gather or send vibrational information (i.e., active space; Mazzoni et al. 2014). Such result is relevant as it potentially affects the ability of insects to detect prey, host or to avoid a predator or parasitoid (Pfannenstiel et al. 1995; Bacher et al. 1996; Meyhöfer et al. 1997; Castellanos & Barbosa 2006; Low 2012; Guedes et al. 2012; Fertin & Casas 2007; Wignall & Taylor 2011), or in conspecific interactions, where individuals employ vibration to manage territory and space (Yack et al. 2001; 2014; Fletcher et al. 2006; Scott et al. 2010) or avoid conflicts (Kojima et al. 2012). Furthermore, given the vast number of potential receivers (eavesdroppers, rivals, and others) within a vibrational communication network, such discoveries can have a considerably more pronounced consequence (Virant-Doberlet et al. 2019). However, further study is needed to support up this idea.

The concentration of vibrations on specific regions of the leaf is likely related to the organism's position on leaves. Nevertheless, our results also showed that the vibrations generated by caterpillars crawling or stinkbugs walking were more conspicuous on the border of leaves than in the central region of leaves or close to the petiole. Previous studies have demonstrated how vibration transmission occurs through plant structures and how plant traits affect vibration transmission (e.g., Bell 1980; Michelsen et al. 1982; McVean & Field, 1996; Magal et al. 2000; Casas et al. 2007; Čokl et al. 2004; 2007; Joyce et al. 2014; Polajnar et al. 2012; Podlesnik et al. 2019; Gordon et al. 2019; Velilla et al. 2020). Thus, it is likely that specific leaf traits, such as the presence of leaf veins (Casas et al. 1998; Magal et al. 2000), leaf area, or leaf thickness (Velilla et al. 2020) have affected the propagation of vibration over the entire leaf. This result is important for caterpillars, particularly Noctuidae, since they may seek out less resonant leaf areas to rest throughout the day without being noticed by predators. However, the relationships between the spatial distribution of vibroacoustic parameters and insect behavioral response remain little-explored. We recommend that future studies investigate these vibrations in more detail in natural conditions, which will provide a greater resolution of the vibratory landscape.

Do caterpillars respond to leaf vibrations?

As previously demonstrated, caterpillars live in a noisy world. In such an environment, detecting and responding to leaf vibrations is predicted to be beneficial to organisms living on plant surfaces (Casas et al. 1998; Castellanos & Barbosa 2006; Guedes et al. 2012). We assessed whether the fall armyworm larvae detect and respond to vibrations from abiotic and biotic sources.

Our findings support the hypothesis that fall armyworm larvae are able to detect abiotic and biotic vibrations and respond to them. Caterpillars exposed to abiotic stimuli consistently changed their behavior when exposed to wind and raindrops, regardless of instar. For instance, wind-induced vibrations led caterpillars to crawl more, particularly in the direction of the leaf's border and abaxial portion. In addition, prior to each new crawl, the caterpillar performed a ‘touch around’ activity in which it lifted its thoracic legs and anterior segments and then touched the leaf along its own axis (Table S1), which likely allows the environment inspection. Raindrop-induced vibrations, on the other hand, caused caterpillars to change from ‘crawling' to ‘resting', which also resulted in more time spent in both of these behaviors (Fig 5A). These are important responses, as both abiotic variables (wind and rain) are known to affect the growth and survival of caterpillars (e.g., Chen et al. 2018; 2019). Thus, it is likely that fall armyworm larvae are gathering information about the environment and changing their behaviors accordingly, as a survival strategy. We suspected that the caterpillars' movement toward the abaxial portion of the leaves was an act to find refuge and avoid being blown away by a strong wind gust. Similarly, staying still during raindrops (i.e., resting) may be a behavior that remains anchored to the substrate and avoids being dislodged by the rain.

Our results also support the hypothesis that caterpillars detect and respond to biotic stimuli when approached by a conspecific of the same instar, or a predator. The behavioral responses were not consistent between instars, as first instars did not respond to the approach of a conspecific or predator, whereas caterpillars from second to fifth instars responded. Our findings showed that second to fifth instars displayed different behavioral responses when confronted with conspecifics of the same instar, and predators. Caterpillars exposed to conspecifics spend more time crawling, touching around, or resting, and only a small percentage of their time feeding or defending themselves. In contrast, caterpillars exposed to predators spend more time freezing, feeding, and resting, and only a small proportion engage in other behaviors. Such results suggest that fall armyworm larvae can distinguish between the vibrations produced by the two types of invaders. In the natural environment, caterpillars interact with both competitors and exploiters. Neonates of fall armyworm, for instance, exhibit a highly aggregated spatial distribution on plants, as females lay eggs in large masses (Farias et al. 2008; Santos et al. 2004). However, just after eclosion and in the subsequent instars, the caterpillars disperse, assuming a spatial distribution more random (Farias et al. 2008), which happens because fall armyworm caterpillars exhibit cannibalistic behavior (Sparks 1979; Pierce 1995; Chapman et al. 2000; Andow et al. 2015), which is particularly frequent under low food availability and high population densities (Elgar and Crespi 1992). As a result, only one or very few larvae per plant are typically found (Sparks 1979). Additionally, the fall armyworm larvae are prey and hosts for a variety of predators and parasitoids (Gross & Pair 1986; Zalucki et al. 2002). Therefore, it is not surprising that caterpillars are able to detect and respond to leaf vibrations and face threats in their environments. In contrast to the results with late instars, first instars do not respond to conspecifics or predators. We argue that this is because, as we showed previously, first instars do not generate noticeable vibrations on the leaves while crawling, making it unlikely that other organisms can detect them. Also, early instars do not supply enough food for predatory stinkbugs, which is evidenced by their preference for later instars and pupae of lepidopterans (Vacari et al. 2013). Consequently, it was expected that there would be selection pressure on neonates to respond to predatory-induced vibrations.

Overall, our results provide novel insights into the vibratory landscape of a caterpillar on a leaf scale using spatial analysis and support the hypothesis that fall armyworm larvae can detect and respond to both abiotic and biotic vibrations. It is important to note, however, that other inputs (such as tactile, visual, and chemical cues) can also induce caterpillar behavior responses. We propose that future studies investigate these vibrations in greater depth, maybe using a playback test to reduce the effect of senses other than vibration.

Supplementary information

Supplementary video S1. http://tiny.cc/nzrkuz

Supplementary video S2 http://tiny.cc/pzrkuz

Supplementary video S3 http://tiny.cc/szrkuz

Supplementary video S4 http://tiny.cc/uzrkuz

Supplementary video S5 http://tiny.cc/vzrkuz

Supplementary video S6 – http://tiny.cc/wzrkuz

Supplementary video S7 – http://tiny.cc/xzrkuz

Supplementary video S8 – http://tiny.cc/yzrkuz

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References

Andow, D. A., Farias, J. R., Horikoshi, R. J., Bernardi, D., Nascimento, A. R., & Omoto, C. (2015). Dynamics of cannibalism in equal-aged cohorts of *Spodoptera frugiperda*. *Ecological Entomology*, 40, 229-236. https://doi.org/10.1111/een.12178

Audacity Team (2021). Audacity(R): Free Audio Editor and Recorder. Version 3.0.2. URL: https://audacityteam.org/

Bacher, S., Casas, J., & Dorn, S. (1996). Parasitoid vibrations as potential releasing stimulus of evasive behaviour in a leafminer. *Physiological Entomology*, 21, 33-43. https://doi.org/10.1111/j.1365-3032.1996.tb00832.x

Bacher, S., Casas, J., Wäckers, F., & Dorn, S. (1997). Substrate vibrations elicit defensive behaviour in leafminer pupae. *Journal of Insect Physiology*, 43, 945-952. https://doi.org/10.1016/s0022-1910(97)00058-9

Barth, F. G., Bleckmann, H., Bohnenberger, J., & Seyfarth, E. A. (1988). Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). *Oecologia*, 77, 194-201. https://doi.org/10.1007/BF00379186

Bell, P. D. (1980). Transmission of vibrations along plant stems: implications for insect communication. *Journal of the New York Entomological Society*, 1, 210-216.

Bowen, J. L., Mahony, S. J., Mason, A. C., & Yack, J. E. (2008). Vibration-mediated territoriality in the warty birch caterpillar *Drepana bilineata*. *Physiological Entomology*, 33, 238-250. https://doi.org/10.1111/j.1365-3032.2008.00627.x

Brunsdon, C., & Comber, L. (2019). An introduction to R for spatial analysis and mapping. London: Sage.

Cambardella, C. A., Moorman, T. B., Parkin, T. B., Karlen, D. L., Novak, J. M., Turco, R. F., & Konopka, A. E. (1994). Field-scale variability of soil properties in central Iowa soils. *Soil*

Science Society of America journal, 58, 1501-1511. https://doi.org/10.2136/sssaj1994.03615995005800050033x

Casacci, L. P., Bonelli, S., Balletto, E., & Barbero, F. (2019). Multimodal signaling in myrmecophilous butterflies. *Frontiers in Ecology and Evolution*, 7, 454. https://doi.org/10.3389/fevo.2019.00454

Casas, J., Bacher, S., Tautz, J., Meyhöfer, R., & Pierre, D. (1998). Leaf vibrations and air movements in a leafminer–parasitoid system. *Biological Control*, 11, 147-153. https://doi.org/10.1006/bcon.1997.0593

Casas, J., Magal, C., & Sueur, J. (2007). Dispersive and non-dispersive waves through plants: implications for arthropod vibratory communication. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1087-1092. https://doi.org/10.1098/rspb.2006.0306

Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, 72, 461–469. https://doi.org/10.1016/j.anbehav.2006.02.005

Chapman, J. W., Williams, T., Martínez, A. M., Cisneros, J., Caballero, P., Cave, R. D., & Goulson, D. (2000). Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? *Behavioral Ecology and Sociobiology*, 48, 321-327. https://doi.org/10.1007/s002650000237

Chen, C., Biere, A., Gols, R., Halfwerk, W., van Oers, K., & Harvey, J. A. (2018). Responses of insect herbivores and their food plants to wind exposure and the importance of predation risk. *Journal of Animal Ecology*, 87, 1046-1057. https://doi.org/10.1111/1365-2656.12835

Chen, C., Harvey, J. A., Biere, A., & Gols, R. (2019). Rain downpours affect survival and development of insect herbivores: the specter of climate change? *Ecology*, 100, e02819. https://doi.org/10.1002/ecy.2819

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, 55, 323-334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO;2

Cocroft, R. B., Shugart, H. J., Konrad, K. T., & Tibbs, K. (2006). Variation in plant substrates and its consequences for insect vibrational communication. *Ethology*, 112, 779-789. https://doi.org/10.1111/j.1439-0310.2006.01226.x

Cocroft, R. B., Gogala, M., Hill, P. S. M., & Wessel, A. (2014). Studying vibrational communication, Springer. https://doi.org/10.1007/978-3-662-43607-3 .

Čokl, A., Prešern, J., Virant-Doberlet, M., Bagwell, G. J., & Millar, J. G. (2004). Vibratory signals of the harlequin bug and their transmission through plants. *Physiological Entomology*, 29, 372-380. https://doi.org/10.1111/j.0307-6962.2004.00395.x

Čokl, A., Zorović, M., & Millar, J. G. (2007). Vibrational communication along plants by the stink bugs *Nezara viridula* and *Murgantia histrionica*. *Behavioural Processes*, 75, 40-54. https://doi.org/10.1016/j.beproc.2007.01.003

Deshmukh S.S., Prasanna B.M., Kalleshwaraswamy C.M., Jaba J., & Choudhary B. (2021) Fall Armyworm (*Spodoptera frugiperda*). In: Omkar (eds) Polyphagous Pests of Crops. (pp. 349-372). Springer, Singapore. https://doi.org/10.1007/978-981-15-8075-8_8

De-Vries, P J. (1990). Enhancement of symbioses between butterfly caterpillars and ants by vibrational communication. *Science*, 248, 1104–1106. https://doi.org/10.1126/science.248.4959.1104

Djemai, I., Casas, J., & Magal, C. (2001). Matching host reactions to parasitoid wasp vibrations. *Proceedings of the Royal Society B: Biological Sciences*, 268, 2403–2408. https://doi.org/10.1098/rsbp.2001.1811

Djemai, I., Casas, J., & Magal, C. (2004). Parasitoid foraging decisions mediated by artificial vibrations. *Animal Behaviour*, 67, 567–571. https://doi.org/10.1016/j.anbehav.2003.07.006

Elgar M, Crespi J (1992). Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford

Farias, P. R., Barbosa, J. C., Busoli, A. C., Overal, W. L., Miranda, V. S., & Ribeiro, S. M. (2008). Spatial analysis of the distribution of *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) and losses in maize crop productivity using geostatistics. *Neotropical Entomology*, 37, 321-327. https://doi.org/10.1590/S1519-566X2008000300012

Fertin, A., & Casas, J. (2007). Orientation towards prey in antlions: efficient use of wave propagation in sand. *Journal of Experimental Biology*, 210, 3337–3343. https://doi.org/10.1242/jeb.004473

Fletcher, L. E., Yack, J. E., Fitzgerald, T. D., & Hoy, R. R. (2006). Vibrational communication in the cherry leaf roller caterpillar *Caloptilia serotinella* (Gracillarioidea: Gracillariidae). *Journal of Insect Behavior*, 19, 1-18. https://doi.org/10.1007/s10905-005-9007-y

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7, 1325-1330. https://doi.org/10.1111/2041-210X.12584

Gordon, S. D., Tiller, B., Windmill, J. F., Krugner, R., & Narins, P. M. (2019). Transmission of the frequency components of the vibrational signal of the glassy-winged sharpshooter, *Homalodisca vitripennis*, within and between grapevines. *Journal of Comparative Physiology A*, 205, 783-791. https://doi.org/10.1007/s00359-019-01366-w

Gross Jr, H. R., & Pair, S. D. (1986). The fall armyworm: status and expectations of biological control with parasitoids and predators. *Florida Entomologist*, 502-515. https://doi.org/10.2307/3495383

Guedes, R. N. C., Matheson, S. M., Frei, B., Smith, M. L., & Yack, J. E. (2012). Vibration detection and discrimination in the masked birch caterpillar (*Drepana arcuata*). *Journal of Comparative Physiology A*, 198, 325-335. https://doi.org/10.1007/s00359-012-0711-8

Gullan, P.J., & Cranston, P.S. (2014). The insects: An outline of Entomology, John Wiley & Sons Ltd.

Hill, P.S.M. (2009). How do animals use substrate-borne vibrations as an information source?. Naturwissenschaften 96, 1355–1371. https://doi.org/10.1007/s00114-009-0588-8

Hill P.S.M., Virant-Doberlet M., & Wessel A. (2019) What Is Biotremology? In: Hill P., Lakes-Harlan R., Mazzoni V., Narins P., Virant-Doberlet M., Wessel A. (eds) Biotremology: Studying Vibrational Behavior. Animal Signals and Communication, vol 6. (pp. 15-25). Springer, Cham. https://doi.org/10.1007/978-3-030-22293-2_2

Isaaks E.H., & Srivastava, R.M. (1989) An Introduction to Applied Geostatistics, Oxford University Press, New York.

Joyce, A. L., White, W. H., & Medina, R. F. (2014). Host plants impact courtship vibration transmission and mating success of a parasitoid wasp, *Cotesia flavipes* (Hymenoptera: Braconidae). *Evolutionary Ecology*, 28, 361-372. https://doi.org/10.1007/s10682-013-9682-7

Kasten, J.R.P., Precetti, A.A.C.M., & Parra, J.R.P. (1978) Dados biológicos comparativos de *Spodoptera frugiperda* (J.E. Smith, 1797) em duas dietas artificiais e substrato natural. *Revista de Agricultura*, 53, 69-78.

Kojima, W., Ishikawa, Y., & Takanashi, T. (2012). Deceptive vibratory communication: pupae of a beetle exploit the freeze response of larvae to protect themselves. *Biology Letters*, 8, 717-720. https://doi.org/10.1098/rsbl.2012.0386

Low, C. (2012). An experimental test of the seismic behaviors of *Antispila nysaefoliella* (Lepidoptera: Heliozelidae) to vibrational stimuli. *Florida Entomologist*, 95, 16–20. https://doi.org/10.1653/024.095.0103

Magal, C., Schöller, M., Tautz, J., & Casas, J. (2000). The role of leaf structure in vibration propagation. *The Journal of the Acoustical Society of America*, 108, 2412-2418. https://doi.org/10.1121/1.1286098

Mazzoni V., Eriksson A., Anfora G., Lucchi A., & Virant-Doberlet M. (2014) Active Space and the Role of Amplitude in Plant-Borne Vibrational Communication. In: Cocroft R., Gogala M., Hill P., Wessel A. (eds) Studying Vibrational Communication. Animal Signals and Communication, vol 3. (pp. 125-145). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-43607-3_8

McNett, G. D., Luan, L. H., & Cocroft, R. B. (2010). Wind-induced noise alters signaler and receiver behavior in vibrational communication. *Behavioral Ecology and Sociobiology*, 64, 2043-2051. https://doi.org/10.1007/s00265-010-1018-9

McVean, A., & Field, L. H. (1996). Communication by substratum vibration in the New Zealand tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). *Journal of Zoology*, 239, 101-122. https://doi.org/10.1111/j.1469-7998.1996.tb05440.x

Meyhöfer, R., Casas, J., & Dorn, S. (1994). Host location by a parasitoid using leaf miner vibrations - characterizing the vibrational signals produced by the leaf mining host. *Physiological Entomology*, 19, 349–359. https://doi.org/10.1111/j.1365-3032.1994.tb01062.x

Meyhöfer, R., Casas, J., & Dorn, S. (1997). Vibration-mediated interactions in a host-parasitoid system. *Proceedings of the Royal Society B: Biological Sciences*, 264, 261–266. https://doi.org/10.1098/rspb.1997.0037

Michelsen, A., Fink, F., Gogala, M., & Traue, D. (1982). Plants as transmission channels for insect vibrational songs. *Behavioral Ecology and Sociobiology*, 11, 269-281. https://doi.org/10.1007/BF00299304

Montezano, D. G., Sosa-Gómez, D. R., Specht A., Roque-Specht, V. F., Sousa-Silva, J. C., Paula-Moraes, S. D., Peterson, J.A. & Hunt, T. E. (2018). Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *African Entomology*, 26, 286-300. https://doi.org/10.4001/003.026.0286

Mortimer, B. (2017). Biotremology: do physical constraints limit the propagation of vibrational information? *Animal Behaviour*, 130, 165-174. https://doi.org/10.1016/j.anbehav.2017.06.015

Pfannenstiel, R. S., Hunt, R. E., & Yeargan, K. V. (1995). Orientation of a hemipteran predator to vibrations produced by feeding caterpillars. *Journal of Insect Behavior*, 8, 1–9. https://doi.org/10.1007/BF01990965

Pierce, N. E. (1995). Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists' Society*, 49(4), 412-453.

Podlesnik, J., Klokočovnik, V., Lorent, V., & Devetak, D. (2019). Prey detection in antlions: Propagation of vibrational signals deep into the sand. *Physiological Entomology*, 44, 215-221. https://doi.org/10.1111/phen.12295

Polajnar, J., Svenšek, D., & Čokl, A. (2012). Resonance in herbaceous plant stems as a factor in vibrational communication of pentatomid bugs (Heteroptera: Pentatomidae). *Journal of the Royal Society interface*, 9, 1898-1907. https://doi.org/10.1098/rsif.2011.0770

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

RStudio Team (2021). RStudio: Integrated Development for R. RStudio Inc. Retrieved from http://www.rstudio.com/

Santos, L. M. D., Redaelli, L. R., Diefenbach, L. M. G., & Efrom, C. F. S. (2004). Fertilidade e longevidade de *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) em genótipos de milho. Ciência Rural, 34, 345-350. https://doi.org/10.1590/S0103-84782004000200002

Scott, J. L., Kawahara, A. Y., Skevington, J. H., Yen, S. H., Sami, A., Smith, M. L., & Yack, J. E. (2010). The evolutionary origins of ritualized acoustic signals in caterpillars. *Nature communications*, 1, 1-9. https://doi.org/10.1038/ncomms1002

Sparks, A. N. (1979). A review of the biology of the fall armyworm. *Florida Entomologist*, 82-87. https://doi.org/10.2307/3494083

Šturm R., Polajnar J., & Virant-Doberlet M. (2019) Practical Issues in Studying Natural Vibroscape and Biotic Noise. In: Hill P., Lakes-Harlan R., Mazzoni V., Narins P., Virant-Doberlet M., & Wessel A. (eds) Biotremology: Studying Vibrational Behavior. Animal Signals and Communication, vol 6. (pp. 125-148). Springer, Cham. https://doi.org/10.1007/978-3-030-22293-2_8

Sueur, J. (2018). Sound analysis and synthesis with R. Cham: Springer.

Tishechkin, D. Y. (2007). Background noises in vibratory communication channels of Homoptera (Cicadinea and Psyllinea). *Russian Entomological Journal*, 16, 39-46.

Travassos, M. A., & Pierce, N. E. (2000). Acoustics, context and function of vibrational signalling in a butterfly-ant mutualism. *Animal Behaviour*, 60, 13–26. https://doi.org/10.1006/anbe.1999.1364

Turchen, L.M.; Cosme-Jr, L.; Yack, J.E.; Guedes, R.N.C. (In press). Bug talk trends & biases: literature survey and meta-analyses of vibratory sensing and communication in insects. *Entomologia Generallis*. https://doi.org/10.1127/entomologia/2021/1380

Vacari, A. M., De-Bortoli, S. A., Goulart, R. M., Volpe, H. X., Otuka, A. K., & Veiga, A. C. (2013). Comparison of eggs, larvae, and pupae of *Plutella xylostella* (Lepidoptera: Plutellidae) as prey for *Podisus nigrispinus* (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America*, 106, 235-242. https://doi.org/10.1603/AN11190

van Griethuijsen, L. I., & Trimmer, B. A. (2014). Locomotion in caterpillars. *Biological Reviews*, 89, 656-670. https://doi.org/10.1111/brv.12073

Velilla, E., Polajnar, J., Virant-Doberlet, M., Commandeur, D., Simon, R., Cornelissen, J. H., Ellers, J. & Halfwerk, W. (2020). Variation in plant leaf traits affects transmission and detectability of herbivore vibrational cues. *Ecology and Evolution*, 10, 12277-12289. https://doi.org/10.1002/ece3.6857

Virant-Doberlet, M., & Cokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33, 121-134. https://doi.org/10.1590/S1519-566X2004000200001

Virant-Doberlet, M., Kuhelj, A., Polajnar, J., & Šturm, R. (2019). Predator-prey interactions and eavesdropping in vibrational communication networks. *Frontiers in Ecology and Evolution*, 7, 203. https://doi.org/10.3389/fevo.2019.00203

Wan, J., Huang, C., Li, C. Y., Zhou, H. X., Ren, Y. L., Li, Z. Y., Xing, L. S., Zhang, B., Qiao, X., Liu, B., Liu, C.H., Xi, Y, Liu, W.X., Wang, W.K., Qian, W.Q., Mckirdy, S., Wan, F.H. (2021). Biology, invasion and management of the agricultural invader: Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Journal of Integrative Agriculture*, 20, 646-663. https://doi.org/10.1016/S2095-3119(20)63367-6

Wignall, A. E., & Taylor, P. W. (2011). Assassin bug uses aggressive mimicry to lure spider prey. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1427–1433. https://doi.org/10.1098/rspb.2010.2060

Wignall, A. E., Jackson, R. R., Wilcox, R. S., & Taylor, P. W. (2011). Exploitation of environmental noise by an araneophagic assassin bug. *Animal behaviour*, 82, 1037-1042. https://doi.org/10.1016/j.anbehav.2011.07.038

Yack, J. E., Smith, M. L., & Weatherhead, P. J. (2001). Caterpillar talk: acoustically mediated territoriality in larval Lepidoptera. *Proceedings of the National Academy of Sciences*, 98, 11371-11375. https://doi.org/10.1073/pnas.191378898

Yack, J. E., Gill, S., Drummond-Main, C., & Sherratt, T. N. (2014). Residency duration and shelter quality influence vibratory signalling displays in a territorial caterpillar. *Ethology*, 120, 354-364. https://doi.org/10.1111/eth.12210

Yack J. (2016) Vibrational Signaling. In: Pollack G., Mason A., Popper A., & Fay R. (eds) Insect Hearing. Springer Handbook of Auditory Research, vol 55. (pp. 99-123). Springer, Cham. https://doi.org/10.1007/978-3-319-28890-1_5

Yack, J. E., & Yadav, C. (*In press*) Vibratory sensing and communication in caterpillars. In: Hill P., Mazzoni, V., Stritih, P., Virant-Doberlet M., Wessel A. (eds) Biotremology: Physiology, Ecology and Evolution.

Yadav, C., Guedes, R. N. C., Matheson, S. M., Timbers, T. A., & Yack, J. E. (2017). Invitation by vibration: recruitment to feeding shelters in social caterpillars. *Behavioral Ecology and Sociobiology*, 71, 51. https://doi.org/10.1007/s00265-017-2280-x.

Zalucki, M. P., Clarke, A. R., & Malcolm, S. B. (2002). Ecology and behavior of first instar larval Lepidoptera. *Annual Review of Entomology*, 47, 361-393. https://doi.org/10.1146/annurev.ento.47.091201.145220

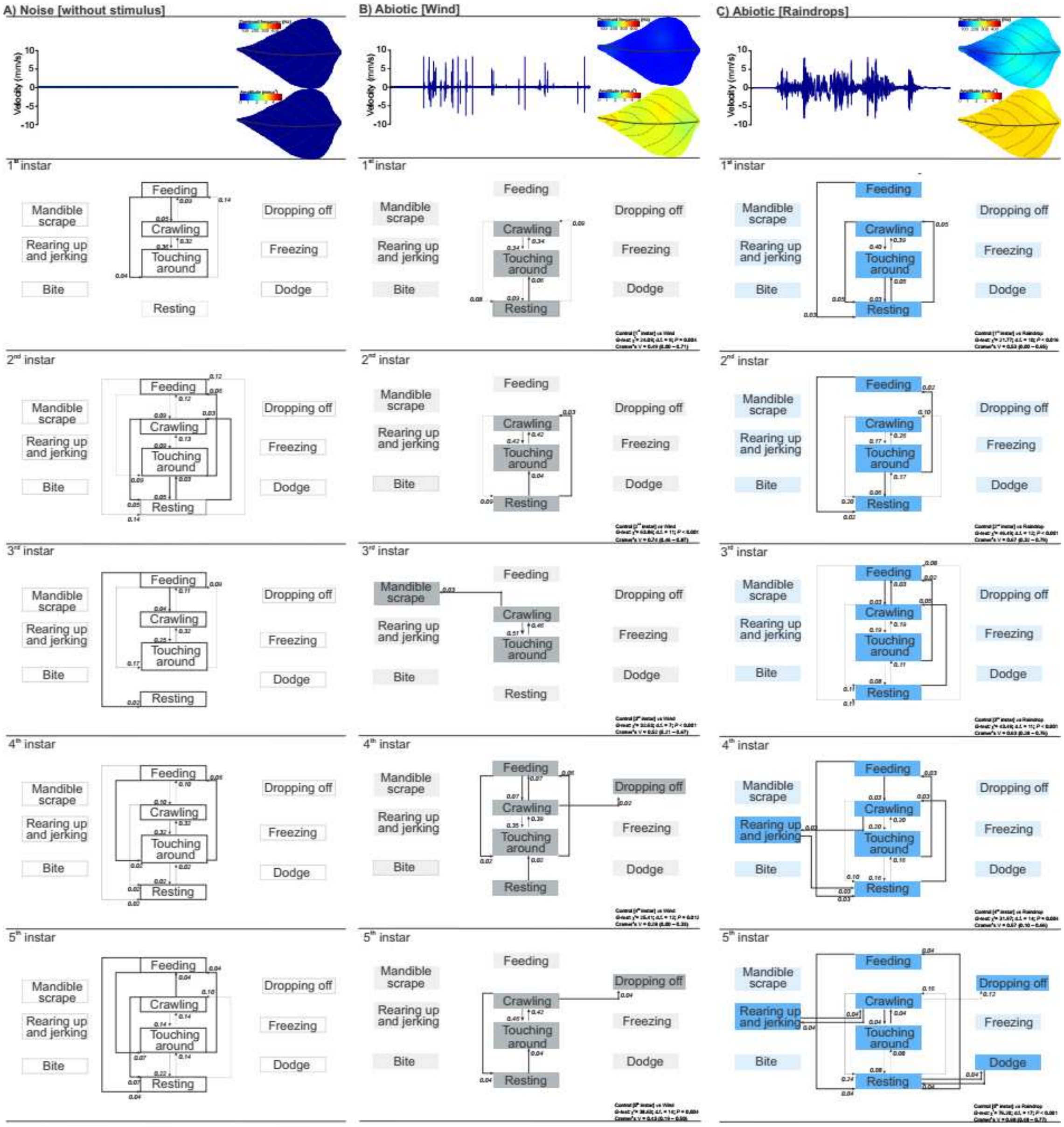

Fig S1. Illustration superior refers to waveforms and spatial distribution of dominant frequency (Hz) [top-right leaves] and amplitude (mm.s-1) [bottom-right leaves] through the bean leaf when exposed to background noise (A), wind (B), and raindrops (C). Ethograms below refer to the response of caterpillars of 1st until 5th instar of fall armyworm when exposed to each stimulus. Ethograms are represented as first-order transition diagrams. The solid arrows indicate each behavioral transition, and the relative thickness of each arrow represents the frequency of each behavior transition. Dark color boxes indicating the observed behaviors, while light color boxes refer to non-observed behaviors. Statistic values refer to the G–test of independence and Cramer's V.

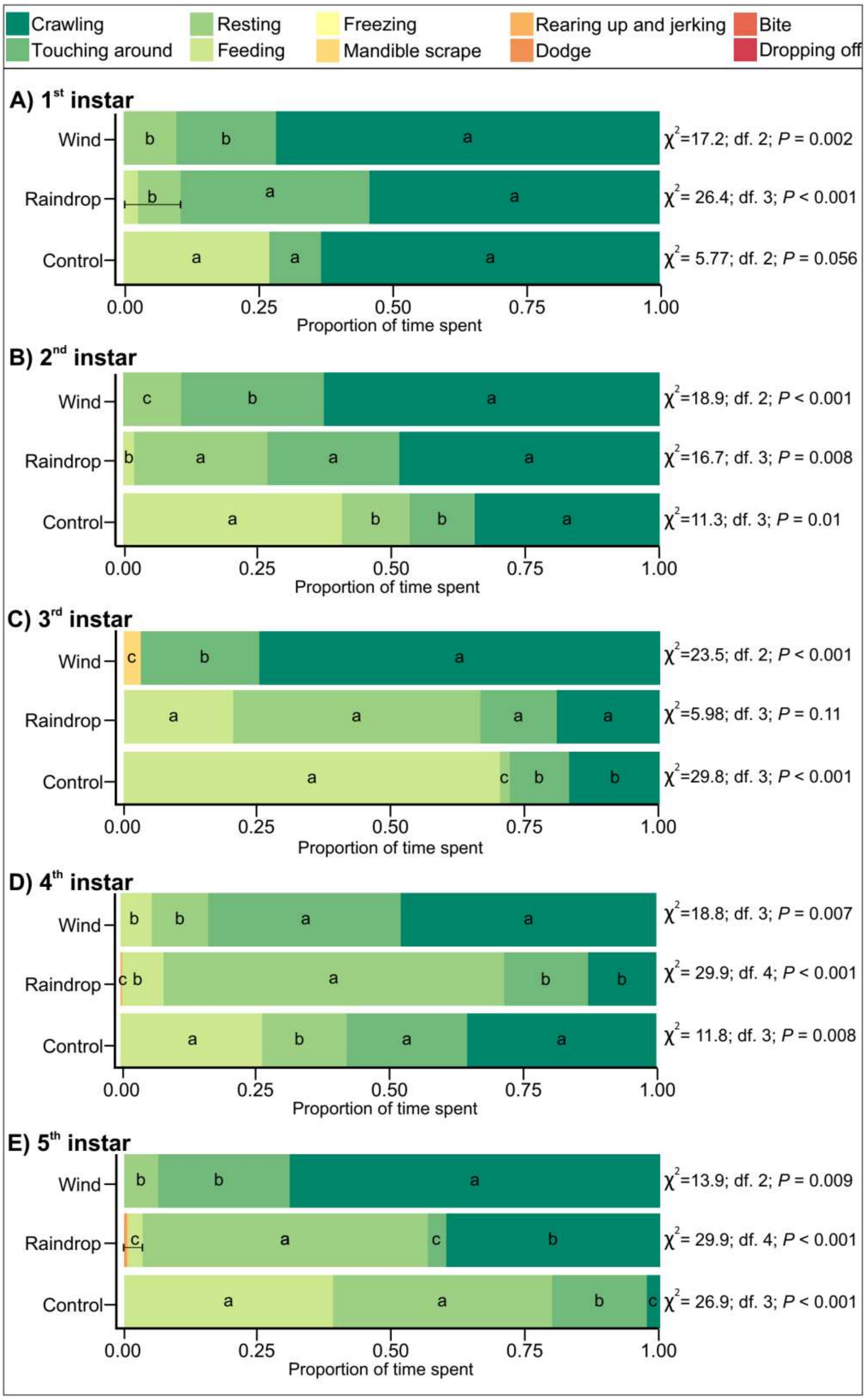

Fig. S2. Time budget spent in each behavior when caterpillars of 1st instar (A), 2nd instar (B), 3rd instar (C), 4th instar(D), and 5th instar (E) of fall armyworm were exposed to simulated wind and raindrops. The proportion of time spent within each stimulus was submitted to Kruskal–Wallis test by ranks. Different letters within the box indicate significant differences by contrast using the criterium Fisher's least significant difference (P < 0.05).

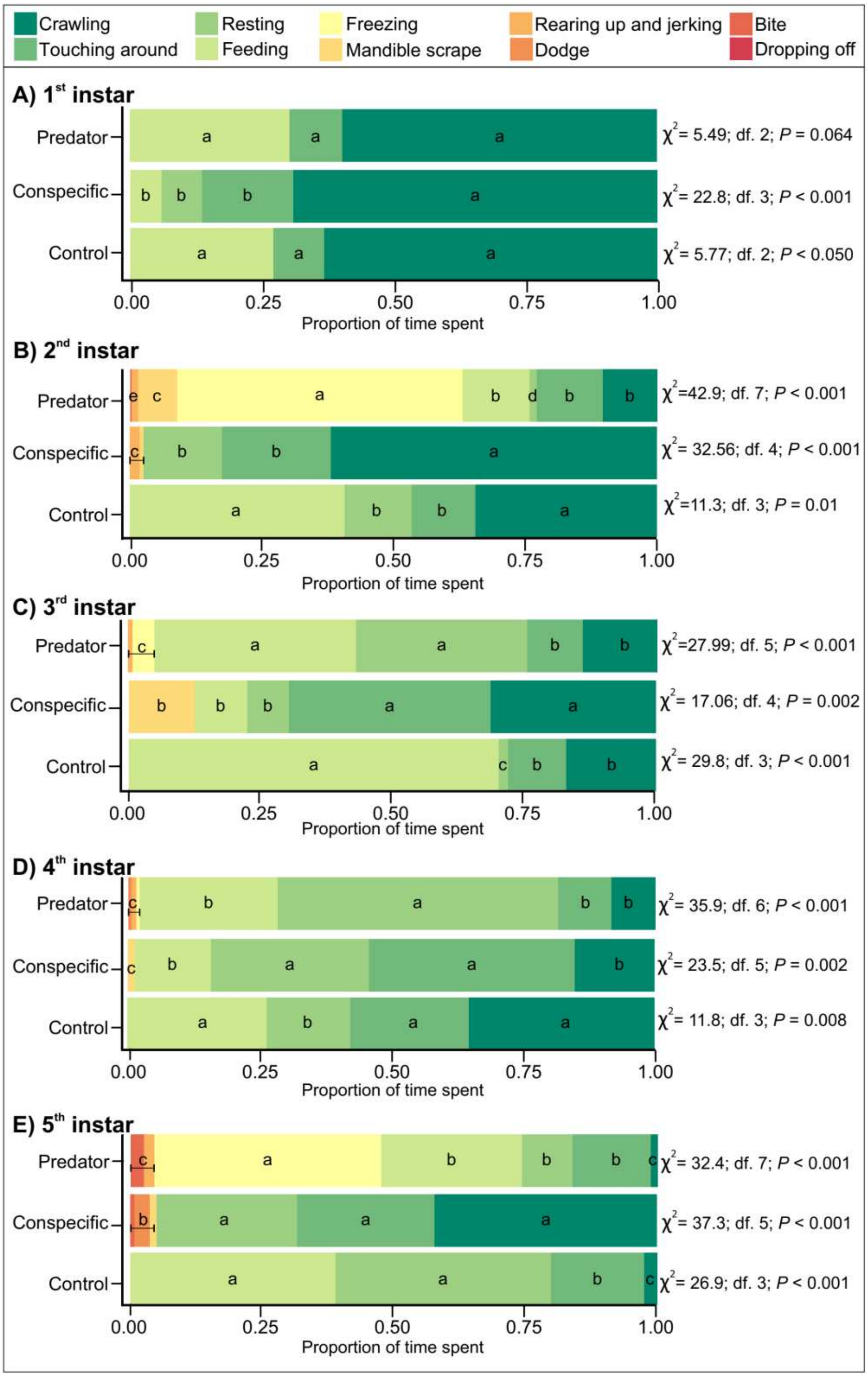

Fig. S3. Time budget spent in each behavior when caterpillars of 1st instar (A), 2nd instar (B), 3rd instar (C), 4th instar(D), and 5th instar (E) of fall armyworm were exposed to the biotic stimulus. The proportion of time spent within each stimulus was submitted to Kruskal–Wallis test by ranks. Different letters within the box indicate significant differences by contrast using the criterium Fisher's least significant difference (P < 0.05).

Table S1. Behavioral categories used to classify behaviors in video records.

Behavior	**Description**
Crawling	Focal animal crawls on substrate (Supplementary video S1)
Resting	Focal animal remains stationary at the same place (Supplementary video S2)
Touching around	Focal animal lifts thoracic legs and anterior segments, then it touches the leaf around itself, circling its own axis (Supplementary video S3)
Feeding	Focal animal chews the leaf (Supplementary video S4)
Dropping off	Focal animal jumps out (or drops off) the leaf (Supplementary video S5)
Freezing	Focal animal encounters another organism, and it responds by "freezing up" or in other words by staying completely still. (Supplementary video S6)
Dodge	Focal animal avoids larva or stinkbug by turning away from another individual. (Supplementary video S7)
Bite	Focal animal bites another larva or stinkbug (Supplementary video S8)
Mandible scrape	Focal animal scrapes laterally its mandibles repeatedly on the substrate. (Supplementary video S5)
Rearing up and jerking	Focal animal lifts thoracic legs and anterior segments followed by a convulsive movement with the head or whole body for both sides. (Supplementary video S8)

Table S2. Semivariogram models and parameters of the dominant frequency and amplitude data used for spatial analyses.

Vibroacoustic parameters	Stimulus	Models	Nugget (C_0)	Partial sill (C)	Sill ($C_0 + C$)	Range (cm)	LSD $C_0/(C+C_0)$	R^2
Dominant frequency (Hz)	Control	Spherical	1.05	8.41	9.46	2.47	0.11	0.86
	Wind	Spherical	0.52	4.16	4.68	2.47	0.11	0.56
	Raindrop	Gaussian	0.79	6.35	7.14	2.47	0.11	0.28
	1st instar	Spherical	1.58	12.62	14.20	2.47	0.11	0.28
	2nd instar	Exponential	1.44	11.50	12.94	2.47	0.11	0.10
	3rd instar	Spherical	1.51	12.11	13.62	2.47	0.11	0.56
	4th instar	Spherical	1.41	11.29	12.70	2.47	0.11	0.82
	5th instar	Spherical	1.66	13.31	14.97	2.47	0.11	0.68
	Stinkbug	Spherical	0.31	2.49	2.80	2.47	0.11	0.81
Amplitude ($mm.s^{-1}$)	Control	Spherical	0.04	0.34	0.38	2.47	0.11	0.75
	Wind	Spherical	0.08	0.63	0.71	2.47	0.11	0.46
	Raindrop	Spherical	0.15	1.16	1.31	2.47	0.11	0.46
	1st instar	Exponential	0.17	1.36	1.53	2.47	0.11	0.40
	2nd instar	Spherical	0.13	1.01	1.14	2.47	0.11	0.52
	3rd instar	Spherical	0.16	1.32	1.48	2.47	0.11	0.58
	4th instar	Spherical	0.10	0.77	0.87	2.47	0.11	0.35
	5th instar	Spherical	0.13	1.07	1.20	2.47	0.11	0.81
	Stinkbug	Spherical	0.03	0.25	0.28	2.47	0.11	0.61

FINAL CONSIDERATIONS

The findings of this Ph.D. thesis provide new insights on the vibroacoustic of insects. First, they highlight significant gaps in the literature, recommending that future research should focus on a broader range of orders and higher taxa, including the importance of vibration in diverse adaptive settings and how both adults and juveniles use vibrations. These findings also give new perspectives into a caterpillar's vibratory landscape on a leaf scale, demonstrating that complex vibratory environments exist even on a tiny scale. It also supports the hypothesis that in order to live, fall armyworm larvae can perceive and respond to both abiotic and biotic vibrations.