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Opinion

Bridging biotremology and chemical ecology: a new terminology

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Living organisms use both chemical and mechanical stimuli to survive in their environment. Substrate-borne vibrations play a significant role in mediating behaviors in animals and inducing physiological responses in plants, leading to the emergence of the discipline of biotremology. Biotremology is experiencing rapid growth both in fundamental research and in applications like pest control, drawing attention from diverse audiences. As parallels with concepts and approaches in chemical ecology emerge, there is a pressing need for a shared standardized vocabulary in the area of overlap for mutual understanding. In this article, we propose an updated set of terms in biotremology rooted in chemical ecology, using the suffix '-done' derived from the classic Greek word 'δονέω' (pronounced 'doneo'), meaning 'to shake'.

Highlights

Living organisms use substrate-borne vibrations for interacting with their environment, where vibrational signals and cues can evoke a diverse range of responses, leading to benefits or detriments for the sender and/or receiver based on the context.

Vibrational signals mediate a variety of animal behaviors, and, notably, plants can gain crucial information by detecting vibrations caused by herbivores, sometimes resulting in the establishment of mutualistic interactions with insects.

Drawing inspiration from the terminology established in chemical ecology, we propose the introduction of the terms 'pherodones' for intraspecific interactions and 'allelodones' for interspecific interactions.

Biotremology: studying a ubiquitous phenomenon

A few years ago, **biotremology** (see Glossary) was established as a distinct scientific discipline from bioacoustics [1] because of unique characteristics of biotremological systems, including morphological, sensory, and physiological aspects distinct from sound-based communication [2,3]. This distinction enables us to integrate comparative studies into biotremology by considering plant-based physiological responses to substrate-borne vibrations produced by both biotic and abiotic factors and phenomena like vibration-induced rapid hatching responses, buzz pollination, and aquatic biotremology [4,5].

Animals relying on vibrations have evolved specialized organs for emission and reception, with physiology hinging on dedicated sensors and metabolic pathways. Furthermore, the use of vibrations requires an adaptation to the constraints imposed by material properties and the limited active space of **vibrational signals**, which primarily propagate through substrate continuity [6,7]. This has resulted in very strong associations between animals and their environment that maximize the effectiveness of communication in their habitat.

Vibrational signals can mediate a wide range of behavioral interactions, and vibrational communication networks involve a myriad of taxa [8], characterizing ecosystems and connecting animal communities, including those previously considered poorly or not connected at all [9]. Vibrational communication is widely used by both vertebrates and invertebrates, and it extends to plants and possibly fungi [10]. In fact, in contrast to the prevailing earlier view that considered them as passive entities, plants can extract valuable information from vibrations [11].

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Evident parallelism with chemical ecology

Pheromones have been a cornerstone in pest management for over 50 years with the introduction of monitoring traps, while the registration of the first mating disruption product took place in 1978 [12]. Currently, pheromone-based pest control strategies (e.g., mating disruption and attract-and-kill) are widespread and well known. Vibrational behavior and communication, though developed along with chemical signaling in the early Metazoa in ancient times, only recently was formally termed 'biotremology' by Endler [13]. Chemical ecology, however, has a long tradition dating back to the 19th century beginning with the first studies by Fabre [14].

The term 'pheromone' was coined 80 years later by Karlson and Lüscher [15]. Pheromones, classified as '**semiochemicals**', were soon applied for pest control [16], and a dedicated terminology was subsequently developed. The term 'pheromone' literally combines the classic Greek φέρειν (pronounced pherein), meaning 'to transfer', and ὅρμαο (pronounced ormao, from which the suffix '-mone' is derived), related to the concept of hormone, to refer to chemical compounds, usually volatiles, emitted by a species to communicate with another individual of the same species. Pheromones are classified based on their effects on behavior (e.g., sexual attraction, alarm, and aggregation). Later, the suffix '-mone' was also extended to chemical compounds that mediate interspecific interactions, termed **allelochemicals** [17]. These are classified based on the respective benefit/detriment to the sender and/or receiver: 'allomones' benefit the emitter, 'kairomones' benefit the receiver [18], and 'synomones' involve mutual benefit [19,20]. These categorizations can easily be applied to other sensory modalities. Recently, vibrations and sounds that mediate animal behaviors have been included in the category of '**semiophysicals**' together with light and colors [21]. The time is now ripe to enrich the lexicon by introducing and aligning a compatible terminology for biotremology to promote collaboration with chemical ecology in areas of associated behavioral interactions.

The need for new terminology in biotremology

To effectively communicate and bridge gaps between scientists within and across disciplines, it is crucial to continue to establish a standardized terminology in biotremology (Box 1 and Figure 1, Key figure). A proper nomenclature ensures clear and effective communication by providing consistent terminology that helps in expressing concepts with precision and clarity while minimizing ambiguity. As experienced in the field of chemical ecology, a standardized terminology facilitates more effective collaboration among researchers from different fields. This is particularly true when considering that multimodal communication in animals and in their interactions with plants is the rule and not the exception, and, consequently, the adoption of a shared terminology would

Box 1. Terminology and definitions of vibrational stimuli

The new terminology proposed here for vibrational stimuli relevant in behavioral ecology is based on the established terminology used in chemical ecology. It incorporates the suffix '-done' from the classical Greek 'δονέω' (pronounced 'doneo'), which means 'to shake'. Examples for each class are described in the main text and are illustrated in Figures 1 and 2 in main text.

Pherodones: substrate-borne vibrational signals that are emitted by an organism and mediate intraspecific interactions. Examples include alarm, mating, territoriality, aggregation, and parental care.

Allelodones: substrate-borne vibrations that mediate interspecific interactions. Based on the effects on emitter and receiver, allelodones can be further categorized into the three following classes: (i) kairodones, substrate-borne vibrations emitted by an organism that evoke a behavioral or physiological response in the receiver that is beneficial to the receiver but not to the emitter; (ii) allodones, substrate-borne vibrations emitted by an organism that evoke a behavioral or physiological response in the receiver that is beneficial to the emitter but not to the receiver, and (iii) synodones, substrate-borne vibrations emitted by an organism that evoke a behavioral or physiological response in the receiver that is beneficial to both the emitter and receiver.

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Key figure

New terminology in biotremology: examples of pherodones and allelodones, designating intraspecific and interspecific vibrational stimuli, respectively

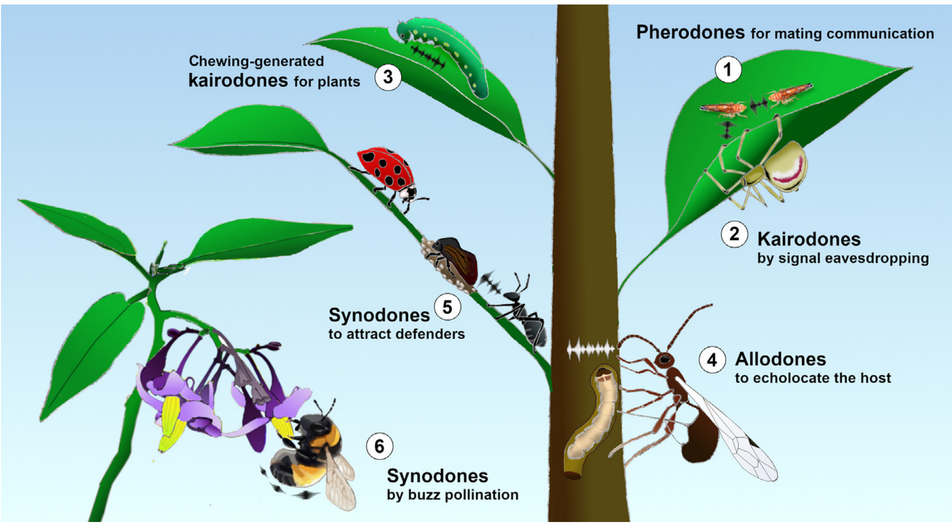

Figure 1. Leafhoppers (e.g., *Scaphoideus titanus*) use (1) pherodones for mating communication. Another species (i.e., a spider predator) may locate them by eavesdropping on their signals, which serve as (2) kairodones. In the case of insect–plant interactions, vibrations induced by chewing larvae can serve as (3) kairodones for plants, activating defensive metabolic pathways. Some parasitoids (e.g., *Pimpla turionellae*) 'echolocate' hosts hidden by drumming a plant surface, emitting vibrations that bounce to the host as (4) allodones. In a mutualistic relationship, when attacked by a predator, treehoppers (*Publilia concava*) emit vibrational signals serving as (5) synodones to attract ants and ensure protection against predators. Another example of synodones is buzz pollination, which allows bees to extract a higher amount of pollen from certain flowers by rapidly vibrating their flying muscles (6). Drawing by R.N. and M.V.R.S.

enhance cross-modal collaborations, benefiting both basic and applied research. Moreover, in the case of applied biotremology, a standardized terminology linked to terms already familiar in chemical ecology would also enhance the comprehension and acceptance of vibration-based solutions for pest control by stakeholders, such as policymakers, industries, farmers, and governmental institutions.

Biological roles of pherodones

Similar to semiochemicals, vibrational signals act as semiophysicals to mediate many behaviors in various animal taxa, including vertebrates and invertebrates (Figure 2). In the case of pherodones, such signals are often species, sex, or even caste specific, and slight variations in their spectral and/or temporal pattern can dramatically affect the final outcome (e.g., male or female choice). Typical pherodones have regular temporal patterns with regular duty cycles and harmonic structure. By contrast, allelodones, which act interspecifically, are often endowed with a comparatively broader variability, irregular temporal patterns, and broadband spectra. The literature on this subject is extensive, although not exhaustive, and for more detailed information, we refer readers to dedicated reviews (e.g., [22]). Vibrational stimuli often operate in a multimodal manner combined with other sensory modalities, such as in strict association with pheromones [23–25]. However, here, we will primarily focus on behaviors that are driven by substrate-borne vibrations. The aim

Glossary

Allelochemicals: semiochemicals that mediate interactions between individuals of different species. There are different types of allelochemicals depending on the costs and benefits for the emitter and receiver. For example, kairomones are eavesdropping chemicals, where the receiver exploits the chemical of the emitter who is using it intraspecifically. Egg parasitoids are known to eavesdrop on (anti)sex pheromones of their hosts to locate host eggs, sometimes hitching a ride on the host to reach oviposition sites [68].

Biotremology: the scientific discipline that studies interactions between organisms that are mediated by substrate-borne mechanical waves (Rayleigh, Sholte, Love, and bending waves), which propagate along the boundary between two media. The clear distinction between biotremology and bioacoustics is that sound is carried as compressional mechanical waves or pressure waves, and the sound signals stimulate an ear, which is essentially a pressure receiver, or pressure-difference receiver [69]. In biotremology, the mechanical waves that carry signals and cues do so through particle displacement that does not involve detection of pressure changes by the wide variety of vibration-based receiving organs [1].

Pheromones: semiochemicals that convey information between individuals of the same species. There are different types of pheromones, such as sex pheromones that are used between two sexes. The first sex pheromone was identified in the silkmoth *Bombyx mori*, a long-chain hydrocarbon called bombykol [70].

Semiochemicals: a class of chemicals that conveys information between organisms, influencing their behavior or physiology. Such information-carrying chemicals are also called infochemicals, although recently the latter term has been used more broadly to include hormones as information-carrying chemical compounds within an individual [71].

Semiophysicals: a class of physical stimuli, such as substrate-borne vibrations, sounds, and lights, that convey information between organisms, influencing their behavior or physiology in a manner parallel to semiochemicals.

Vibrational signals: mechanical oscillations or movements produced by

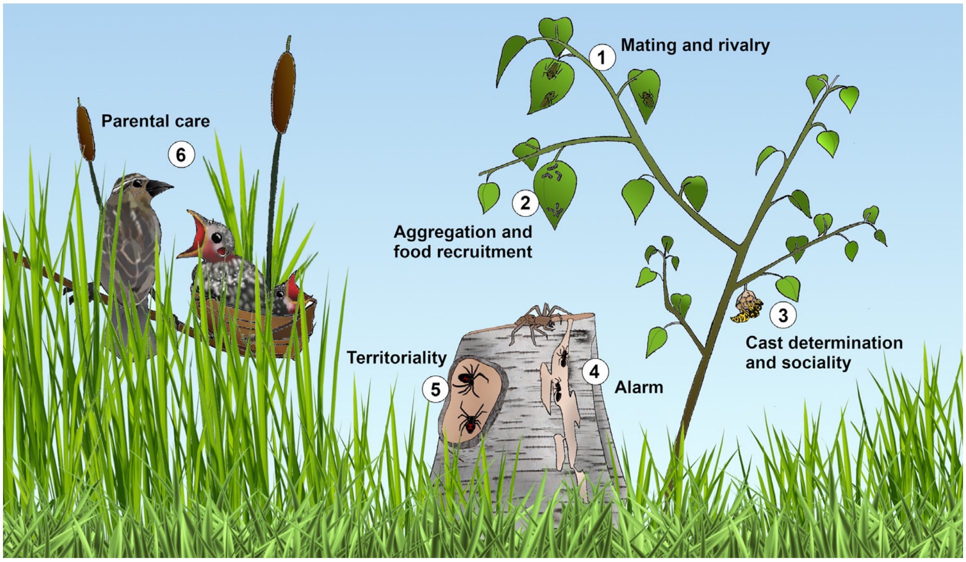

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Figure 2. Biological role of pherodones. (1) Leafhoppers (e.g., *Scaphoideus titanus*) rely on vibrational signals for mating and rivalry. (2) Group-living caterpillars (e.g., *Drepana arcuata*) use vibrations for aggregation and food recruitment. (3) Drumming behaviors in paper wasps (*Polistes fuscatus*) contribute to caste determination and sociality. (4) Alarm behavior in ants (*Camponotus* spp.) is communicated through drumming on nest walls. (5) Black widows (*Latrodectus hesperus*) use abdominal vibrations for territoriality to maintain distance. (6) Flexible nest material in red-winged blackbirds (*Agelaius phoeniceus*) enables the transmission of vibrations indicating the arrival of a parent with food. Drawing by R.N. and M.V.R.S.

an organism as a means of communication with conspecifics or other species transmitted through a substrate along media boundaries.

of this section is to provide a few illustrative examples that clarify the association with the respective terminology and parallel with analogous behaviors in chemical ecology [26].

Sexual behavior: mating pherodones and rivalry pherodones

The use of vibrational signals for sexual communication is widespread and can involve the establishment of a male–female duet. In pherodones, duets are often characterized by strict temporal rules that confer high species specificity to the communication. For example, in leafhoppers, such as *Scaphoideus titanus*, a male and a female engage in a vibrational duet after the initial male calling signal. Such a duet begins with the initial identification duet, progresses through the female's location duet, and concludes with mating following the courtship duet. Intriguingly, when a male eavesdrops on the duet of another pair, it assumes the role of a rival and emits a different pherodone, called disturbance noise, which interrupts the ongoing communication [27]. Contrary to the common belief that pheromones are released by one sex or in the absence of a proper duet, behaviors parallel to the male–female courtship duet in biotremology have also been observed in chemical ecology. For example, in various Lepidoptera and Hymenoptera species, one gender emits a sex attractant pheromone to lure the other gender from a distance, and then the latter releases a short-range courtship pheromone, initiating the courtship process [28,29].

Territorial pherodones

Possession of territory, whether it is a piece of land, a leaf, or a spider web, can be determined by the emission of vibrational signals that inform antagonists about the strength and quality of the signaler. Such pherodones function to discourage potential antagonists from staying in the area delimited by the signal active space. Examples include kangaroo rats (*Dipodomys phillipsii*) drumming the ground with their feet to repel potential intruders [30], female black widows (*Latrodectus hesperus*) emitting abdominal vibrations as warning signals to maintain a respectful distance between individuals, thus avoiding physical combat [31], and male red-eyed tree frogs (*Agalychnis callidryas*) tremulating to send threatening plant-borne vibrations to other males to maintain calling territories [32].

Alarm pherodones

The rapid transmission of an alarm signal through a group of conspecifics is crucial and can mean the difference between life and death. Examples are numerous across animals and include the following: the stingless bee (*Axestotrigona ferruginea*) that emits guarding vibrations to alert companions when encountering non-nestmates [33], ants of the genus *Camponotus* that emit vibrations by drumming their mandibles and abdomen on the plant surface [34], and elephants (*Loxodonta africana*) that can even discriminate between familiar and unfamiliar seismic alarm signals, the latter perceived as a nonreliable source of information [35].

Food recruitment and aggregation pherodones

Cooperative food signaling after an individual locates a profitable food site allows for rapid recruitment with high benefit for the whole community. This phenomenon is present in eusocial insects such as ants, which stridulate when encountering a food source [36], and in honeybees, which perform a 'tremble dance' as a counterpart to the 'waggle dance'. Unlike the 'waggle dance' that increases recruitment, the 'tremble dance' serves to limit the number of recruitments [37]. It also applies to gregarious and subsocial species such as treehoppers that emit specific vibrational signals at a suitable feeding site [38]. Other examples are found in sawfly larvae and other gregarious caterpillars that advertise to conspecifics [39,40].

Adult–offspring interactions

Vibrational signals can be an important element of communication between parents and offspring. In treehoppers, nymphs signal to call adults in the presence of potential threats (e.g., predator wasps) [41]. Parent–embryo communication in the true bug (*Parastrachia japonensis*) mediates egg hatching synchronization to avoid cannibalism [42]. Egg hatching can also be regulated by the cracking of eggshells, which triggers the immediate hatching of the neighboring eggs [43]. In the case of the red-winged blackbird (*Agelaius phoeniceus*), nests constructed from flexible substrates enable nestlings to readily express begging behaviors in response to vibrational cues that can indicate the arrival of a parent bearing food [44]. Similarly, in hornets (*Vespa orientalis*), the 'hunger signal' is a vibration produced by hungry larvae scraping the nest surface to summon workers for food provision [45].

Sociality

Social insects rely heavily on communication to maintain and coordinate their complex social organizations. Recent research has revealed the important role of pherodones in several species [46,47]. In honeybees, sexually immature drones are subject to vibrational signals from workers, possibly to promote development and mating performance [48]. In *Polistes* wasps, adults emit vibrations by drumming their antennae on the paper nest, which inhibits diapause in larvae that will develop into workers. This action contributes to caste determination, influencing gene expression in developing individuals [49,50]. Therefore, pherodones can have both 'primer' (long-lasting physiological changes) and 'releaser' (immediate behavioral responses) functions, much like analogous pheromones [51].

Biological roles of allelodones

For many animals, survival depends on interactions with individuals of different species. To this end, nonconspecifics can mimic vibrational signals or eavesdrop on incidental vibrational cues (e.g., walking or grooming) as they play a predator role or avoid predation. In these contexts, these signals or cues serve as allelodones. However, when the same signals and cue are used in a conspecific role to disrupt courtship or sneak matings, they can simultaneously function as pherodones.

Kairodones

Interspecific interactions where the benefit accrues to the receiver at the expense of the emitter are common in the fields of predator–prey and host–parasitoid relationships. Examples are found among parasitoids and predators that determine the exact position of their hosts and prey on the plant (i.e., leaves, fruit, and bark) by eavesdropping on the vibrations produced by them while chewing or moving [52]. It has also been demonstrated that the chewing of caterpillars can induce activation of metabolic responses in plants associated with chemical defenses [53]. Notably, pherodones can also be exploited as kairodones by specialized receivers: both predators and parasitoids can locate their targets by eavesdropping on their mating signals [9,54]. Alarm signals can also be classified as kairodones, as observed with ants attacking mammalian browsers, which emit vibrations while feeding on acacia plants [55], or snakes biting anuran eggs, thereby triggering an earlier hatching in an attempt by the embryos to evade predation [56]. A similar hatching trigger has been observed in reptiles [57].

Allodones

Typical examples of allodones, where the emitter but not the receiver benefits, are lycaenid caterpillars that infest ant nests, mimicking queen signals to gain acceptance and nourishment from the workers [58], or kangaroo rats that footdrum at snakes as a means of deterrence [59]. In general, all distress signals aimed at deterring hostile organisms [22] belong to this category. The 'echolocation' typical of parasitoids that drum the surface of a plant tissue to detect the presence of larvae and pupae of the host species [60] can therefore also be considered an allodone.

Synodones

Synodones are a class of interspecific vibrational signals where the benefit is reciprocal to the emitter and the receiver. A textbook case of a synodone is buzz pollination, where vibrations are produced by certain bumblebees during their 'buzz' when attached to a flower [61]. This mechanism is particularly beneficial for flowers with tightly packed or enclosed anthers, as the vibrations induce a substantial release of pollen. The mutualism arises from the efficient release by the flower and its subsequent collection by the bumblebee. Another example of a mutualistic relationship involving synodones occurs when ants respond to specific vibrational signals emitted by female treehoppers during encounters with predators. This prompts the ants to provide protection for the female and her offspring, and they ultimately receive honeydew as a food reward [62].

Concluding remarks and future perspectives

Aligning terminology used in the same context among groups of nonconspecifics, even those using vastly different mechanisms, is a prerequisite for a discipline to establish itself and gain interest and eventual recognition within the scientific community. The approach used in this article could easily be extended to other semiophysicals, such as sounds and light. However, in biotremology, this extension is particularly urgent in the applied component because of its aspiration to play a significant role in the fields of plant protection and pest control [63]. In this regard, in 2022, the European market welcomed a bimodal trap for the brown marmorated stink bug, *Halyomorpha halys*, representing a significant advancement in pest control by combining aggregation pheromones for long-range attraction with vibrational signals for short-range efficacy [64]. In addition, the intersection of biotremology with digital agriculture is leading to the development of promising solutions (i.e., vibrational mating disruption and pest infestation monitoring and control)

Outstanding questions

Function

What is the specificity level of plants' responses to substrate-borne vibrations?

Can pherodones of key pests elicit a specific response in their host plants?

Evolution

How have pheromones and allelodones evolved across different taxa?

How far back does the coevolution of synodones go?

What are the roles of the substrate and the individual in the evolution of substrate-borne signals?

Ecology and conservation

How do environmental vibrations (both natural and anthropogenic) influence pherodones of single species or species communities?

What do pherodone profiles of species communities tell us about ecosystem health?

Causation

How do substrate-borne vibrations influence the metabolism and physiology of animals and plants?

What is the mechanism by which substrate-borne vibrations elicit a priming effect on plants?

Development

What are the physical limits to the production and application of pherodones?

Do pherodones change with individual development over time? What is the sensitive learning stage of the receiver?

Regulative aspects

How could pherodones be included in the current regulations for crop protection?

What are possible risks, if any, for the environment, including side effects for nontarget organisms?

applied to several crop pests (e.g., leafhoppers, whiteflies, psyllids, and bark beetles) [25,65–67]. This convergence exemplifies the synergistic potential of merging language from otherwise seemingly diverse fields. The development of a new vocabulary is crucial to facilitate the acceptance of various stakeholders, including policymakers who require access to appropriate terminology to delineate clear objectives, formulate laws and regulations, and prepare scientific calls. The success of pheromone-based strategies in sustainable pest control can be partly attributed to the familiarity of the term 'pheromone', which immediately identifies the nature and function of the releasing dispensers and associated methods (e.g., mating disruption and monitoring). Therefore, the introduction of 'pherodone' aims to facilitate the general acceptance and comprehension of the mechanism of action of devices that transmit vibrations into plants, simultaneously attributing a character of environmental safety. In addition, we acknowledge the importance of pairing basic and applied research; therefore, we wish this vocabulary to be ultimately adopted also in other fields of biotremological studies for a more nuanced understanding of vibrational communication in insect–plant systems at multitrophic levels but also to underscore the pivotal role of multidisciplinarity in modern sciences (also see Outstanding questions).

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Declaration of interests

No interests are declared.

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