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Opinion

Plant ecoacoustics: a sensory ecology approach

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Many interactions of plants with the environment have an acoustic component, including the actions of herbivores and pollinators, wind and rain. Although plants have long been tested for their response to single tones or music, their response to naturally occurring sources of sound and vibration is barely explored. We argue that progress in understanding the ecology and evolution of plant acoustic sensing requires testing how plants respond to acoustic features of their natural environments, using methods that precisely measure and reproduce the stimulus experienced by the plant.

Highlights

Plants can detect many features of their environment, including vibration.

A plant's natural acoustic environment contains information potentially crucial to fitness, and recent work shows that natural acoustic stimuli can elicit relevant responses.

We propose an experimental approach focused on what plant tissues experience, using methods that precisely measure and reproduce the actual acoustic energy received by the plant.

This experimental approach provides a general framework for understanding how plants perceive and use acoustic energy in their environment.

Plants detect acoustic information

Plants are expert at sensing their external environment. They can detect gravity, touch, light, chemicals, temperature, electromagnetic forces, and sound, all without specialized sensory organs [1]. Many sources of **mechanical waves** (see Glossary) cause a **vibration** of plant tissues, ranging from the calls of birds and insects to the activity of herbivores and pollinators and the action of wind and rain. But for **acoustic** sensing, the information plants gain from their natural environment, and how this information influences plant fitness, is less well known than for the better-studied sensing of light, gravity, touch, and airborne chemicals. The task now for the field of plant **ecoacoustics** is to arrive at the most useful conceptual framework and methodological approaches for understanding the role of acoustic sensing in the life of plants.

Until recently, the study of plant acoustics has relied on computer-generated sounds as experimental stimuli, such as single tones or music. And indeed, a large body of experimental work in agriculture has determined the optimal frequencies and amplitudes of broadcast tones for influencing particular aspects of plant growth. This responsiveness to tones might occur if natural acoustic stimuli contain components of the artificial acoustic stimuli. Crop plants can respond to single, airborne tones with changes in gene expression, hormone levels, seed germination, growth, disease, fruit ripening, and drought resistance [2–9]. This research reveals a fascinating range of sound-responsive plant traits. But why have plants evolved the ability to make decisions about growth, defense, and reproduction based on sound? To answer that question, we need to know what acoustic stimuli plants receive in nature and how plants make use of them.

We argue that progress in plant ecoacoustics requires two changes in emphasis. The first is a shift away from human-generated stimuli and toward relevant natural stimuli in the plant's environment, coupled with the measurement of ecologically relevant plant traits. The second is a shift away from relying on our human **umwelt**, in which the perception of **airborne sound** plays a central role. A more plant-centered approach recognizes that what plants experience is the vibration of their leaves, stems, and roots and that we should use methods that precisely measure and reproduce the actual **substrate-borne vibrations** experienced by the plant. These changes will

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place plant acoustics within the field of **sensory ecology**, the study of how organisms perceive and interact with their environment [10].

The plant's acoustic environment

The substrate vibrations occurring in a given place and time have been called the **vibroscape** [11]. This term was initially coined for vibration-sensitive insects that live on plants and communicate using plant-borne vibrations. The vibroscape is an extremely useful concept for plant ecoacoustics because it focuses the discussion on the plant's sensory world rather than our own. Here, we refer to an individual plant's vibroscape as the vibrations occurring within the plant's stems, roots, leaves, flowers, and fruits.

Plant vibroscapes contain real-time information relevant to plant fitness (Figure 1). For example, the interactions of a plant with its arthropod community each have a vibrational signature. Herbivores produce characteristic vibrations (Figure 1B–D): the rhythmic crunching of a caterpillar eating a leaf, the plant-borne song of a sap-feeding leafhopper, and the scraping of a walking beetle. Mutualists likewise generate vibrations when interacting with the plant (Figure 1E–G): the wingbeats of an approaching pollinator, the cacophony of vibration as the pollinator moves over the flower, the plant-shaking hum of buzz pollination, and the light, rapid footsteps of an ant visiting a nectary. Other vibrations (Figure 1H–J) originate at a distance from the plant. Leaves are good absorbers of airborne sound [12], and the result is that leaf vibrations reproduce the local soundscape: singing birds, human conversations, traffic sounds, and wind. For insects living on plants, wind-induced vibrations constitute a major source of vibrational noise that rises and falls with each passing gust [13]. Anthropogenic noise is also part of the vibroscape of many plants. Traffic noise can reach levels damaging to urban plants [14] and seagrasses are affected by low-frequency, anthropogenic vibrations [15].

What is the evidence that plants can perceive acoustic cues in their environment and respond to them? We first consider how plants use acoustic cues associated with herbivory. The vibrations produced by leaf-feeding insects such as caterpillars are an unavoidable consequence of their feeding behavior: each closure of their mandibles generates a high-amplitude burst of vibration. Caterpillars close their mandibles repeatedly, typically several times per second, with each closure removing a small piece of leaf tissue. The acoustic signature of this feeding activity is characteristic and, to our ears, immediately recognizable as feeding, regardless of the species of caterpillar or plant [16].

Two species of plants have been tested so far for their responses to caterpillar feeding vibrations, and both responded by increasing their chemical defenses. When thale cress (*Arabidopsis thaliana*) plants were exposed to intermittent feeding vibrations recorded from a feeding caterpillar of the cabbage butterfly (*Pieris rapae)*, the plants increased the concentration of one chemical defense (glucosinolates) in a dose-dependent manner, with higher concentrations at greater vibration amplitudes [17]. In response to feeding vibrations, these plants also increased the concentrations of phenolic defenses in their leaves, produced wound-signaling hormones, and altered their production of volatile organic compounds upon subsequent attack [17,18]. Cultivated tobacco plants (*Nicotiana tabacum*) likewise increased the concentration of nicotine in leaves stimulated by the feeding vibrations of a leaf-mining moth larva [19].

A. thaliana plants mounted a similar response to the feeding vibrations of two different caterpillar species [18]. This lack of discrimination among different sources of leaf-feeding vibrations, coupled with the acoustic similarity among feeding vibrations from a wide range of plant and insect species, suggests that chewing vibrations may provide a consistent acoustic cue that allows plants to recognize attacks by an entire guild of herbivores [18].

Glossary

Acoustic: related to sound or hearing; in plants, this relates to the ability to detect vibration.
Airborne sound: pressure waves that travel through the air; sometimes called airborne vibrations, especially when involving particle flow near the sound source.
Ecoacoustics: the study of the relationships of organisms and their environment mediated through sound; sometimes called acoustic ecology or soundscape studies.
Mechanical wave: oscillation of a medium that transfers energy away from a source.
Sensory ecology: the study of how organisms acquire and process information from the environment, and of how ecological factors shape the evolution of sensory systems.
Substrate-borne vibrations: mechanical waves propagating within a structure; when they occur in plants, they are called plant-borne vibrations.
Umwelt: the features of the environment perceived by an organism.
Vibration: oscillation of the particles of a structure or medium, often due to propagating mechanical waves.
Vibroscape: the set of substrate vibrations occurring in a given environment.

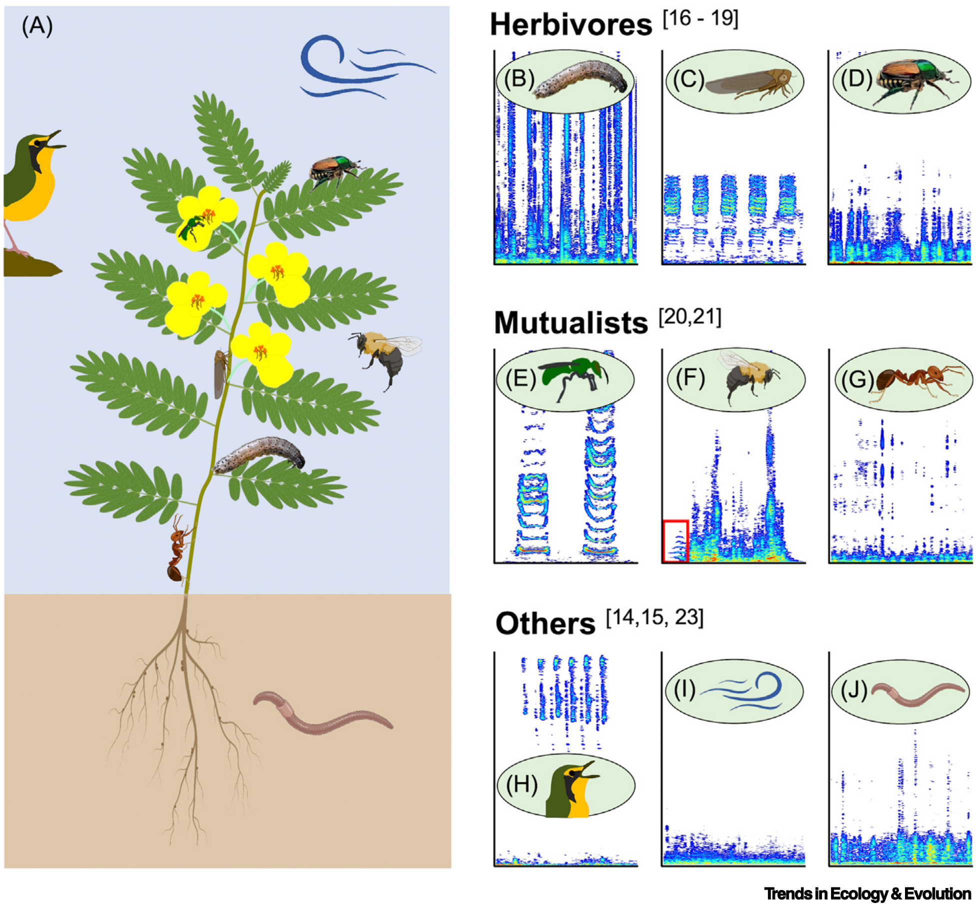

Figure 1. The vibroscape of an herbaceous annual plant, the partridge pea (*Chamaecrista fasciculata*), with illustrations of vibration sources (A), and spectrograms of their associated vibrations (B–J). Herbivores [16–19]: (B) Feeding by a fall armyworm caterpillar (*Spodoptera frugiperda*); (C) singing by an unidentified leafhopper; (D) walking by a Japanese beetle (*Popillia japonica*). Mutualists [20,21]: (E) Buzz pollination by a halictid bee (*Augochlora* sp.) recorded on the stem 5 cm from the flower; (F) visit to a depleted flower by a common eastern bumblebee (*Bombus impatiens*) – note brief flight-induced vibrations as the bee approaches (red box) and the broadband vibrations produced by the bee on the flower; (G) walking by a nectar-harvesting ant (*Aphaenogaster* sp.). Background vibrations [14,15,23]: (H) Airborne sound-induced vibrations by a singing bird (Kentucky Warbler, *Geothlypis formosa*) ~15 m away; (I) wind-induced vibrations; and (J) soil vibrations of a moving common earthworm (*Lumbricus terrestris*), recorded on the plant stem 5 cm above the surface. Recordings were made in the field except for (B), (D), and (J), which were recorded in the laboratory. All spectrograms have a duration of 3 s (x-axis) and a maximum frequency of 5 kHz (y-axis). References cited in the figure indicate effects on plant traits of the corresponding type of vibration source.

Feeding vibrations originate on the plant itself (or on a nearby plant), but other vibrations originate at a distance. Are there vibrations generated by air- or soil-borne sounds that evoke adaptive plant responses? Flowers of beach evening primrose (*Oenothera drummondii*) increased the concentration of nectar when exposed to the flight sounds of honeybees [20]. Although the adaptive value for plants of linking nectar production to wingbeat detection has been questioned [21], this study does reveal that pollinator-associated vibrations can influence floral traits. Another intriguing plant response to vibration is the growth of roots toward a sound source. The root tips of maize (*Zea mays*) seedlings in the water grew toward the source of pure tones [22], and roots of potted pea (*Pisum sativum*) seedlings grew toward the played-back sound of water running in a tube [23]. This response has been hypothesized to play a role in foraging for water

[23], and discoveries about the complexity of soil soundscapes [24,25] raise the possibility of many additional influences on sound-directed root growth.

How selective are plant responses to naturally occurring vibrations, and how is selectivity achieved? To respond adaptively to vibration, plant tissues must match the right response to the right stimulus. This need for selectivity presents a fascinating problem in plant sensing because many of the signals in a plant's vibroscape overlap in some acoustic properties (Figure 1) [11]. One form of selectivity may rely on responding only to stimuli that contain particular frequencies. For example, MSL10 ion channels have a peak response of around 1–2 Hz, which is a good match for the frequencies induced in plants by wind [26]. In another example, the defenses of *A. thaliana* leaves were primed by feeding vibrations with frequencies up to several kHz but not by wind vibrations in the 20–40 Hz range [17]. However, not all differential responses can be explained by a simple frequency filtering mechanism. Defenses of *A. thaliana* leaves were primed by playback of chewing vibrations but not by leafhopper song with a very similar frequency spectrum [17]. That discrimination must rely on other acoustic differences, such as the presence of impulses in the chewing vibrations but not in the leafhopper song.

Plants also produce sound and vibration. Drought-stressed plants produce ultrasonic emissions, at least in part via collapsing water columns in the xylem [27]. The movement of leaves and woody plant parts in the wind can generate acoustic energy [28], and corn seedlings growing in water generate clicks, possibly from the root tips [22]. However, there is no evidence yet that plant acoustic emissions influence the plant or other nearby organisms [29].

Relevant plant responses to measure

To understand why plants use mechanosensory information, it is important to test natural acoustic stimuli (Box 1) and measure ecologically meaningful responses, that is, responses that relate in some way to plant growth, survival, and reproduction. However, plant responses to environmental stimuli are idiosyncratic, in that many kinds of possible responses are species specific, environment specific, and shaped by prior and current experience. As a result, there is no single, correct answer to the question of which plant responses to acoustic stimuli one should measure. Here are some generalities to consider.

Box 1. Measuring and reproducing plant-borne vibrations

Studying plant acoustics involves measuring displacements of plant tissues at frequencies from a few to thousands of times per second, often on a scale undetectable to the human eye [49]. For example, *A. thaliana* leaves increased their glucosinolate defenses in response to displacements of <3 microns [17], a distance much smaller than the diameter of a human hair.

To measure vibrations in a small structure like an *A. thaliana* leaf, a laser vibrometer (Figure IA,B) provides a noncontact method that detects Doppler shifts in reflected light from a cold laser to track the motion of a surface. Video-based methods may eventually provide another suitable noncontact method [50]. Accelerometers are contact sensors suitable for more robust plant structures such as woody stems or larger leaves.

The key experimental method for animal and plant acoustics is the playback. Here, the goal is usually to record the vibrations produced during an event of interest, such as an herbivore feeding on a leaf (Figure IC), and recreate those vibrations on an undamaged leaf of a new plant. For playing back a recorded signal, Figure ID shows a linear resonant actuator with a graphite rod attached to provide an offset from the plant and held in place using a foam ring. Many vibration actuators can accurately reproduce a vibration after filtering imposed by the actuator setup is compensated for and the playback amplitude is adjusted [51,52] to match a desired level (Figure IE). For low-mass plant structures, calibration of the actuator can be done before it is attached to the plant for playback (Figure IF). MATLAB scripts for calculating and applying compensation filters and adjusting amplitude are available from R.C. on request.

Playback of airborne sound can also be used to induce vibrations in plants, with the caveat that the amplitude of leaf motion will depend on not only the stimulus characteristics but also the resonant properties of the plant structure. Accordingly, it is always important to measure and calibrate the vibrations of the targeted plant part. Overall, only if researchers measure the vibrations experienced by the plant will it be possible to build a general model of how plants detect and respond to acoustic features of their environment.

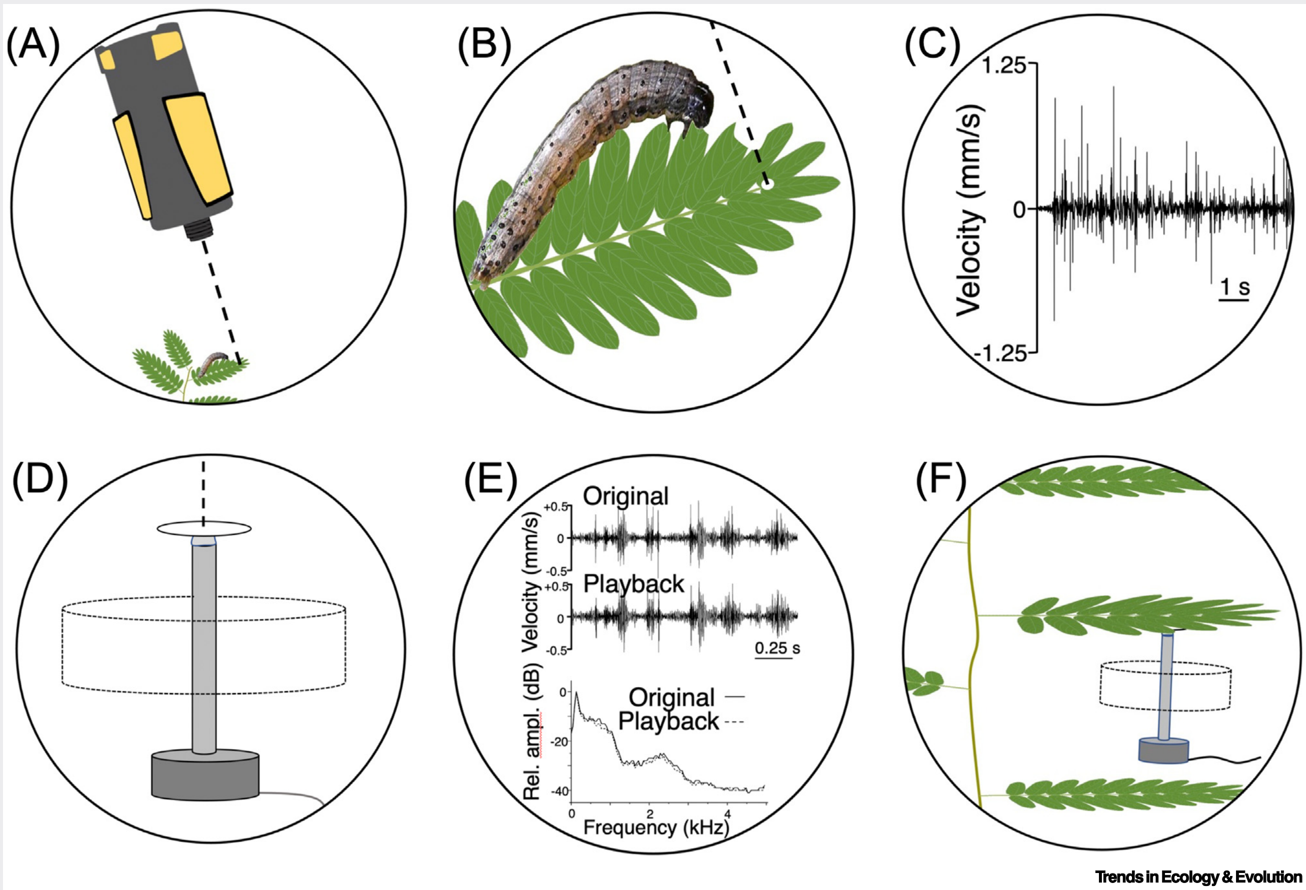

Figure I. Outline of the process for measuring and reproducing a plant-borne vibration.

First, plant responses to naturally occurring pests like herbivores can involve direct responses that are measurable after a single encounter with the pest, and priming which is only detectable as an increased response to subsequent encounters. The literature provides many potentially useful traits to measure if they can be linked to fitness, ranging from early signaling events to inducible chemical and morphological defenses [30,31].

Plant chemical defenses are commonly used as proxies of ecological impacts because they are inducible, often easier to measure than reproduction, and important to pathogen success and herbivore feeding preferences and performance [31,32]. However, in designing these kinds of experiments with insect pests, it is important to remember that plants may produce multiple kinds of chemical defenses [30] because different insect herbivores may respond differently – even oppositely – to specific chemical defenses [33]. This complexity can be minimized by working with a plant species whose chemical defense systems have been characterized and linked to fitness measures.

Plant responses to pollinator visits often cause changes in traits that are direct measures of fitness, such as the number of fruits produced, seeds matured, and seed germination success. Because of their importance to pollinator behavior, proxies of fitness like nectar composition, nectar quantity, and stamen movement are often measured [20,34–36]. However, their relationships to fitness are often assumed rather than demonstrated.

When a direct measure of fitness is not feasible to acquire, we recommend choosing a plant species with a well-characterized set of fitness proxies.

Plant acoustic sensing and within-plant signaling

All life on earth relies on mechanosensing to monitor internal and external mechanical forces critical to survival. Mechanosensing controls plant architecture at multiple scales, with plant growth and development influenced by relatively static mechanical stresses like gravity and by dynamic stresses such as touch and the oscillating motion caused by wind [37,38].

Unlike acoustic sensing in animals which relies on complex sensory structures, plants lack organs that have evolved specifically for acoustic sensing. However, virtually all plant cells contain several types of mechanoreceptors that respond to mechanical stress and play important roles in morphogenesis [37,39,40]. In principle, any living part of a plant can detect acoustic stimuli. For example, plant trichomes (hairs) can relay mechanical stimulation, although the role of specific mechanoreceptors in detecting trichome motion is unstudied [41].

There are several examples of how one mechanoreceptor contributes to plant mechanosensing. MSL10, a member of the plant family of mechanosensitive ion channels of small conductance-like proteins, is required for detection of the low-frequency oscillations caused by wind [26]. MSL10 is also required for transmission of wound signals to other parts of the plant [42]. This systemic signaling provides other plant parts the opportunity to preemptively increase defense.

When a plant receives acoustic cues of herbivory along with tissue damage, the importance of the acoustic component relative to signals generated by damage is unknown. For example, insects generate vibrations from feeding and deposit oral secretions. Tissue damage generates electrical, reactive oxygen, calcium, hydraulic wave, and volatile signals, which either propagate themselves or generate secondary signals that can travel between cells or in the phloem to distant plant parts [43]. Acoustic cues, unlike oral secretion, may be especially useful indicators of insect attack because they can travel through plants at speeds of up to meters per second. This is much faster than speeds measured for electrical signaling, hydraulic waves, or phloem transport [44]. In addition, systemic acoustic cues may be the most reliable indicators of insect attack because damage cues can arise from other causes.

Acoustic signals are important in several pollination syndromes. Bat-pollinated species attract their pollinators by floral morphologies providing acoustic reflection different from those pollinated by insects or hummingbirds [45]. In buzz pollination, anthers only open in response to specific wing beat frequencies of appropriate pollinators [34,35]. Although largely unexplored outside of these two examples, acoustic energy delivered by pollinators may be of broader importance, with one example of changes in nectar concentration in response to airborne sound mimicking that of a pollinator [20]. The vibrational component of plant–pollinator interactions could be a useful early cue for plants to reallocate floral resources important to pollinators.

Concluding remarks

We advocate here for a plant-centered, ecological perspective to plant acoustics, asking how plants sense and use acoustic stimuli in a natural environment. We argue for an experimental approach based on sensory ecology that begins with understanding the mechanosensory information available to the plant during an ecological interaction, then carefully reproduces that

Outstanding questions

The study of plant ecoacoustics is in its infancy, with many critical, unanswered questions. Some of the most pressing questions include the following:

How do plants distinguish among different acoustic stimuli? There is a wide range of variation in spectral and temporal features of the acoustic signals plants experience, and *A. thaliana* distinguishes among at least some of these stimuli.

How is signal detection accomplished in background noise sources such as the vibrations from wind or rain? Work so far has primarily tested plant responses to individual stimuli in a low-noise environment.

What is the active space of vibration within plants? Stimulating one leaf with feeding vibrations can lead to a systemic response elsewhere on the plant.

Is the rapid transmission of vibration an advantage to the plant? Vibrations are transmitted throughout the plant 10–100 times more rapidly than calcium, reactive oxygen species, or electrical signals.

How do vibrations interact with other coincident cues in plant recognition of herbivory? Plants have multiple cues for recognizing an herbivore attack, including damage and oral secretions.

What is the relative importance of different vibrational components of pollinator–flower interactions, like flight sounds and pollinator contact with the flower?

mechanical stimulation in controlled experiments and measures plant responses that are relevant to that interaction. Research with non-natural, computer-generated sound has shown that many plant traits are responsive to acoustic stimulation. However, only an approach grounded in the plant's natural acoustic environment can reveal why plants have evolved the ability to respond to acoustic cues and how they use them (see Outstanding questions).

If plants are shown to detect acoustic information in nature and respond adaptively to relevant cues, it will be critical to understand this fundamental sensory domain of plants. Plant responses to acoustic stimuli may also provide new opportunities to improve agricultural production with fewer chemical inputs [4,6,46–48]. Thus, plant ecoacoustic research can provide not only a fundamental understanding of plant biology but also enhance sustainable agriculture.

Declaration of interests

No interests are declared.

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