Trends in
Plant Science

Opinion

# Plant protection and biotremology: fundamental and applied aspects

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**There is overwhelming evidence that synthetic pesticides have a negative impact on the environment and human health, emphasizing the need for novel and sustainable methods for plant protection. A growing body of literature reports that plants interact through substrate-borne vibrations with arthropod pests and mutualistic arthropods that provide biological control and pollination services. Here, we propose a new theoretical framework that integrates insights from biological control, the ecology of fear, and plant-borne vibrations, to address plant–insect interactions and explore new, sustainable opportunities to improve plant health and productivity.**

## Highlights

Plants use substrate-borne vibrations to interact with both biotic and abiotic factors in their environment.

Substrate-borne vibrations play a key role in the detection of herbivory and the interactions between plants and pollinators.

More than 150 000 species of arthropods, including major pests and carnivores, use plant-borne vibrations for communication, prey detection, and mating.

Biological pest control involves using living organisms to suppress pest populations.

The ecology of fear relates to predator-induced behavior and physiology-mediated costs for prey.

## Need for sustainable plant protection solutions

Modern agriculture relies heavily on the use of synthetic pesticides for crop protection. Despite the positive effects, associated mainly with yield increases, the use and misuse of pesticides have generated several major problems. Pesticide residues have been found in many areas of the environment and are generally considered a major cause of biodiversity loss in managed and natural ecosystems [1,2]. Exposure to pesticides has caused adverse health effects for farmers and consumers via residues on agricultural products [3]. The capacity of many arthropod pests to develop resistance to pesticides has resulted in pest resurgence, leading to significant control failures and huge economic losses [4]. It is increasingly clear that pesticides are not the way to go in agriculture; thus, there is an urgent need for sustainable solutions assuring plant protection and productivity. Here, we propose a multidisciplinary approach that combines **biological pest control** (see Glossary), the **ecology of fear**, and **substrate-borne vibrations**, to shed light on largely overlooked, fundamental interactions between plants, pests, and **natural enemies**. This new multidisciplinary approach may have important practical implications for the development of innovative and sustainable methods to improve plant health and productivity.

## Biological control

Biological control is the use of living organisms, called natural enemies, to suppress populations of pests and weeds below the economic injury level [5,6]. Biological control has found application in agriculture based on the use of predatory insects and mites, insect parasitoids, and pathogenic microorganisms (fungi, bacteria, and viruses) for the regulation of pest populations. Biological control is environmentally friendly, cost-effective, leaves no residues on agricultural products, and there are no known cases of control failure due to pest resistance to natural enemies [7].

**Augmentative biological control** is based on the release of mass-reared natural enemies to control pests (Figure 1). It is currently used in over 30 million ha worldwide in greenhouse and open field crops [7]. Augmentative biological control is usually applied in the framework of **integrated pest management (IPM)**, a strategy for plant protection that prioritizes nonchemical measures with minimal impact on human health and the environment [8]. Examples of methods and tools used in IPM include crop rotation, plant cultivars that are resistant/tolerant to pests,

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Figure 1. Examples of arthropod natural enemies used in augmentative biological control: a larva of the brown lacewing, *Micromus angulatus,* preying upon an aphid (left); a parasitoid of the genus *Aphidius* laying an egg into its aphid host (right). Original pictures by Ward Stepman with permission to reproduce granted by Biobest Group N.V.

pheromones to trap pests or manipulate their behavior, and, as the last resort, selective chemical pesticides that are compatible with biological pest control methods. Despite the proven value of augmentative biological control, either alone or as part of IPM, there are situations where its efficacy needs to be improved. Examples include pests with explosive population growth, such as aphids and spider mites, invasive pests, and pests with relatively few efficient natural enemies, such as the Colorado potato beetle. Therefore, novel, sustainable methods and smart tools for pest control that can be integrated into IPM are needed [7].

## The ecology of fear: predator-induced stress on their prey

Biological control of arthropods by arthropods is based on the capacity of predators and parasitoids to locate, consume, and reduce the pest populations and eventually plant damage. Nevertheless, the impact of predators on their prey extends beyond predation. Predator-induced stress has been documented in various vertebrate and invertebrate species, including major arthropod crop pests [9,10]. The mere presence of the predator can dramatically alter prey behavior and physiology, resulting in reduced foraging and feeding, lower level of reproduction, and, consequently, lower plant damage (non-consumptive effects of predators on prey) [11–13]. This is referred to as the 'ecology of fear'.

Most research done on cues that mediate interactions between plants and plant-dwelling arthropods has focused on visual and chemical cues used by the herbivorous prey to assess predation risk [11,14,15]. Spider mites laid significantly fewer eggs on leaves previously exposed to chemical cues deposited by their predators [13]. Similarly, the feeding rate of the adult Colorado potato beetle, a major potato pest, was reduced by 23% and plant damage by 64% in experimental plots with risk of predation by the adult spined soldier bug, *Podisus maculiventris* (the authors could not define the nature of the cues causing the reduction in oviposition and plant damage; see our suggestion in Box 1) [11]. Interestingly, non-consumptive effects and reduced plant damage have also been reported for pollinators; air disturbances produced by flying honeybees resulted in decreased feeding and concomitant damage on a plant by caterpillars [16]. In terms

## Glossary

**Augmentative biological control:** release of mass-reared natural enemies to suppress pest populations.
**Bee buzz (for pollination):** combination of substrate-borne vibrations and airborne vibrations (sound) of varying durations, which release mechanical energy to facilitate the opening of the anthers to release the pollen.
**Biological pest control:** use of living organisms to suppress pests and weeds.
**Biotremology:** study of the vibrational interactions among organisms.
**Ecology of fear:** non-consumptive effects of predators on their prey, such as mediated by behavior and physiology.
**Herbivore-induced plant volatiles (HIPVs):** organic compounds emitted by plants in response to feeding or oviposition by herbivores. They have a role in plant defense by attracting carnivorous arthropods.
**Infophysicals (or semiophysicals):** mechanical signals and cues, in particular substrate-borne vibrations, mediating species interactions (in analogy to infochemicals, such as pheromones, kairomones, and allomones, that also mediate species interactions).
**Integrated pest management (IPM):** strategy to protect plants from pests and diseases that prioritizes non-chemical measures with minimal impact on human health and the environment.
**Natural enemies:** living organisms, such as arthropod predators and parasitoids and pathogenic microorganisms (fungi, viruses, and bacteria), used in biological control to suppress pest populations.
**Substrate-borne vibrations:** mechanical waves that, when propagated through plant tissues (e.g., leaves, stems, or roots), are mostly constituted by bending waves.

### Box 1. Potential role of substrate-borne vibrations in interactions between plants, pests, and mutualistic arthropods

Plant defense is metabolically costly. A trade-off between defense and growth exists, known as the dilemma of plants: to grow or to defend [38]. However, Cortés *et al.* proposed that plants may trade direct defenses with indirect defense provided by a predatory arthropod [36]. This was based on results showing that, under conditions of competition for light, the direct defenses of tomato plants mediated through phytohormones and leaf trichomes were suppressed; plants allocated resources to growth. However, the blend of herbivore-induced plant volatiles (HIPVs) emitted by the leaves (i.e., the indirect defenses of the plant) was more attractive for a plant mutualist, the predatory bug *Macrolophus pygmaeus*, compared with the HIPVs from control plants. Given that plants invest in defense as a response to vibrational cues simulating herbivore feeding [30], will plants invest in growth when they perceive substrate-borne vibrations by a beneficial, predatory arthropod? The possibility that plants discern and selectively respond to the plethora of vibrations in their environment [29] is an intriguing question in plant sensory ecology [18]. Yet, to our knowledge, the impact of playback of predator substrate-borne vibrations on plant physiology and phenology has not been studied.

As suggested by Appel and Cocroft [19], 'the vibrational component of plant–pollinator interactions could be a useful early cue for plants to reallocate floral resources important to pollinators'. This is in perfect agreement with the data reported by Pashalidou *et al.* [32], where flowering was significantly accelerated in plants bitten by bumblebees compared with control plants. Interestingly, mechanical damage inflicted on the plants, to try and simulate bumblebee biting, did not result in accelerated flowering. The authors suggested that chemical or other bumblebee-related cues might be causing the earlier flowering. We propose that the mechanical vibrations produced when the bumblebees were interacting with leaves may have had a role in triggering flowering of the plants [33].

In the study by Hermann and Thaler [11], the authors could not explain how the adult prey, which is invulnerable to the predator in their study system, could detect predation risk. We suggest that plant-borne vibrations produced by the spined soldier bug [26] might be an important cue to enable the Colorado potato beetle adults to detect the predator. If this is true, the potential of using predator substrate-borne vibrations to manipulate pest behavior is extremely promising, given that 37% less oviposition, a 23% lower feeding rate, and 64% less plant damage caused by the Colorado potato beetle were recorded in experimental plots with predators enclosed in mesh sleeves [11].

Many of the species of arthropod predators used in augmentative biological control are mass-reared on semi-artificial systems where the natural prey is substituted by a factitious prey [39]. As a result, many species of mass-reared predators are naive regarding the chemical or mechanical cues of their natural prey. Sometimes, this may compromise their efficacy to locate and consume the pest in the field [40]. Previous research has shown that predatory arthropods can learn and utilize olfactory cues emitted by plants to locate their herbivore prey [41]. Arthropod predators (spiders) can also exploit vibrational mating signals to detect their leafhopper prey [42]. The variation in the response to the prey vibrational signals was speculated to be due to the phenotypic plasticity of the spider and its ability to learn. Thus, conditioning of naive predators to the vibrational cues of their prey might enhance their capacity to locate the prey in the field and provide more efficient biocontrol services. This possibility has not yet been explored by the biocontrol industry.

of applied pest control, olfactory predator cues (from, e.g., urine) have been successfully used for the manipulation of vertebrate prey [17], but the application of predator cues against arthropod pests for plant protection has not yet been explored.

## Biotremology: the study of vibrational interactions among organisms

Animals exchange information using visual, chemical, and mechanical signals. Plant-borne vibrations represent ubiquitous, yet overlooked, cues that mediate communication and interactions with their environment in plants and animals [18,19] (Figure 2). Substrate-borne, vibration-mediated interactions are prevalent in terrestrial arthropods [18], including major taxa of plant-dwelling arthropod pests and their natural enemies, such as Hemiptera, Coleoptera, Thysanoptera, Diptera, and Hymenoptera. It is estimated that more than 150 000 species of insects use plant-borne vibrations for communication [18]. Plant-borne vibrations are used by insects as **infophysicals (or semiophysicals)** [20], which provide a wealth of information about vital functions, such as courtship and mating, location of food or prey, and social organization [18,21,22].

Substrate-borne vibrations have been used to protect plants by manipulating insect behavior [21]. In some insect pest species, courtship and mating are mediated by the exchange of

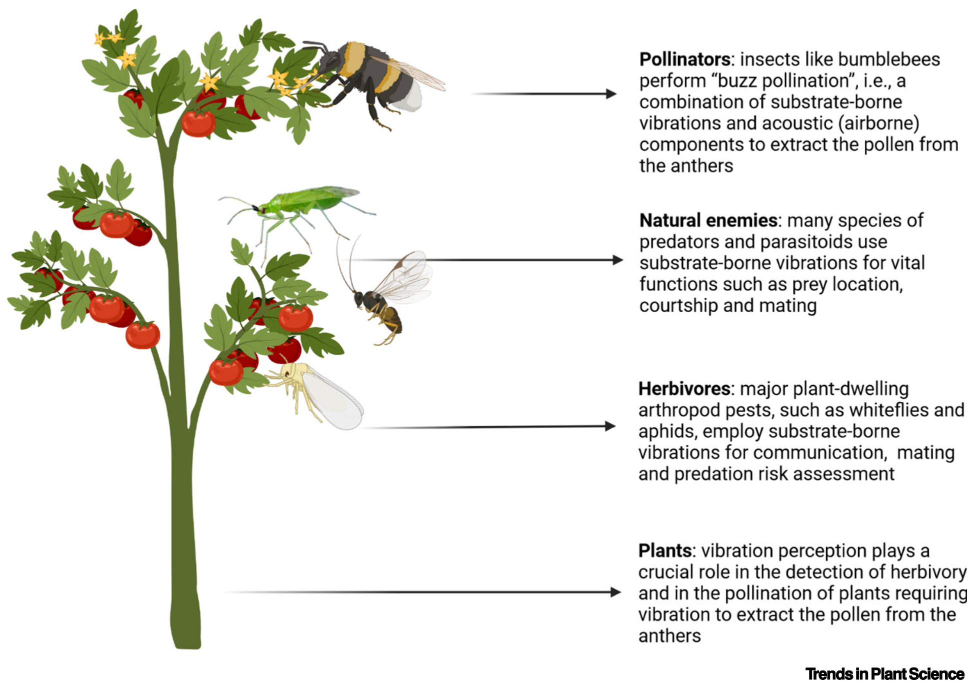


Figure 2. The role of substrate-borne vibrations in the interactions between plants, herbivores, and natural enemies. Major plant-dwelling arthropod pest and natural enemy taxa, such as Hemiptera, Coleoptera, Thysanoptera, Diptera, and Hymenoptera, use plant-borne vibrations for courtship and mating, location of food or prey, predation risk assessment, and social organization [18,20]. Plants also perceive substrate-borne vibrations and respond to them [19]. Substrate-borne vibrations play a crucial role in the detection of herbivory. For instance, playback of the leaf-chewing substrate-borne vibrations by a caterpillar increased the concentration of defensive compounds in arabidopsis (*Arabidopsis thaliana*) [30]. Additionally, vibrations appear to have a crucial role in pollination, especially in those plant species where bees extract the pollen by vibrating the anthers [33]. This is known as 'buzz' pollination, a combination of substrate-borne vibrations and acoustic (airborne) components used by the bees to open anthers and extract the pollen. Created with BioRender (BioRender.com).

vibrational signals. Playback of natural or artificial vibrational signals interferes with pair formation and eventually reduces the population level of subsequent pest generations [23,24]. Substrate-borne vibrations are also used to enhance the attraction of pests to pheromone traps, thus reducing pest populations [25].

However, there are no studies examining the potential of using predator vibrational cues (i.e., amplifying the ecology of fear effect) for pest management. This is rather surprising given that it has long been known that invertebrate prey can not only detect predation risk, but also distinguish in a meaningful way between two predator species based on their distinct substrate-borne vibration profiles [26].

Plants also detect and respond to substrate-borne vibrations, which can be generated by some airborne vibrations [19,27,28]. For example, plant-borne vibrations can mediate the detection of herbivory [29]. Playback of substrate-borne vibrations simulating leaf-chewing by a caterpillar resulted in enhanced induction of plant chemical defense upon herbivory [30]. Furthermore, the production of plant-borne vibrations has a crucial role in the pollination of plant species that require 'buzz pollination'. In these species, bees extract pollen by vibrating the anthers, inadvertently fertilizing the flowers [31–33]. The '**bee buzz**' comprises a combination of substrate-borne vibrations and airborne vibrations of varying durations, which release mechanical energy to facilitate the opening of the anthers to release the pollen. Furthermore, vibration of flowers by bee wing buzzes caused increased nectar flow and concentration [34], although the authors' interpretation of these results was questioned by others [35].

## Hypotheses integrating biological control, the ecology of fear, and biotremology to improve plant health and productivity

We propose an integration of biological control, the ecology of fear, and plant-borne vibrations (**biotremology**) to understand and manipulate interactions between plants, pests, and their natural enemies. Moreover, we argue that important practical implications may arise for promoting plant health, growth, and reproduction. Below, as well as in Box 1 and Figure 3 (Key figure), we provide our hypotheses for each trophic level separately (i.e., plants, arthropod pests, and their natural enemies).

### Key figure

### Hypotheses integrating biological control, the ecology of fear, and biotremology to improve plant health and productivity

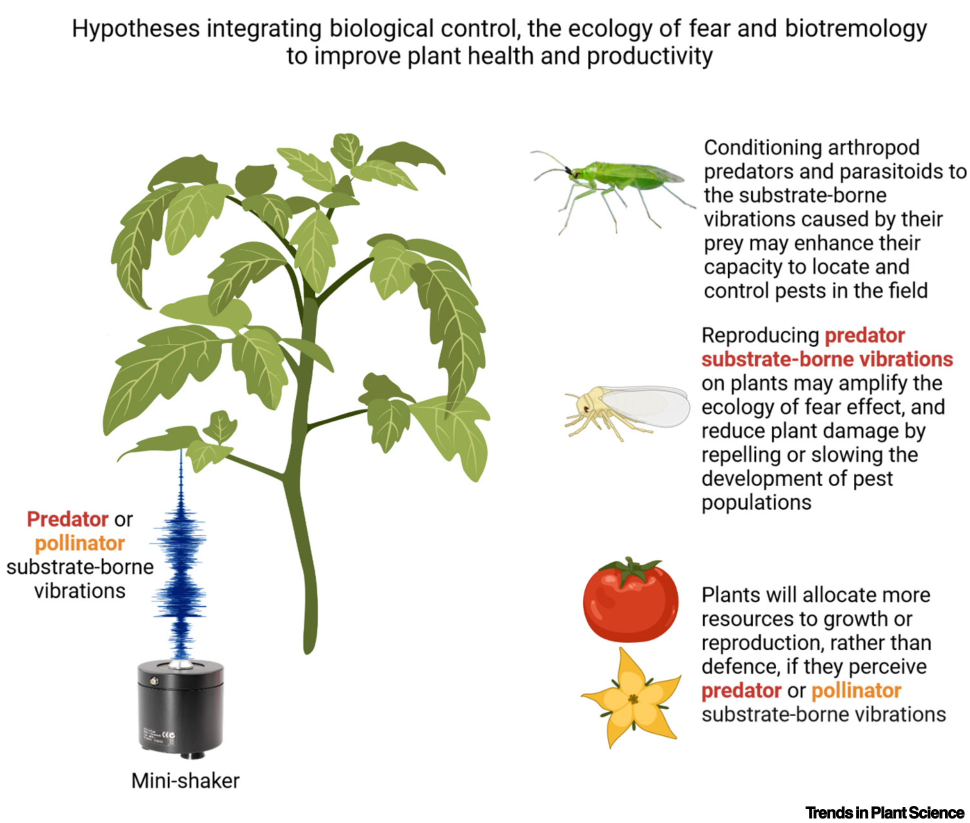


Figure 3. Substrate-borne vibrations of predators, pollinators, or abiotic factors can be recorded using a laser vibrometer (for details, see [43]). Subsequently, they can be accurately reproduced using appropriate equipment, such as mini-shakers. This figure shows a mini-shaker attached to the plant with a rod reproducing substrate-borne vibrations emitted by the predatory arthropod *Macrolophus pygmaeus* [44]. For a detailed description of the hypotheses shown here, please see Box 1. Created with BioRender (BioRender.com).

### Plants

We hypothesize that, if plants respond to substrate-borne vibrations that simulate herbivore feeding by investing in defense [12], they will invest in growth when perceiving substrate-borne vibrations that represent predator presence. Plants will trade direct defenses with the perceived (via the substrate-borne vibrations) indirect defense by carnivore arthropods and, thus, can still invest in growth [36]. This may be possible if there is an evolutionary history between the plant and the predator and if predator substrate-borne vibrations have distinct characteristics that are detectable by the plants. Specifically, we suggest that the playback of predator substrate-borne vibrations on plants with the help of a resonant actuator [19] will: (i) suppress the induction of direct plant defenses; (ii) alter indirect plant defenses (i.e., the blend of **herbivore-induced plant volatiles** that attract predators); and (iii) enhance plant growth and reproduction.

Buzz pollination involves the production of high-intensity substrate-borne vibrations, and we suggest that these vibrations not only cause the target flower to release pollen, but are also transmitted to neighboring flowers and other plant parts [37]. Mechanoreception of these transmitted vibrations by other parts of the plant may influence the timing or amount of pollen production, flower maturation, and eventually plant reproduction.

### Arthropod pests

We suggest that pests will avoid settling on plants that are connected to 'transmitters' (actuators) of predator substrate-borne vibrations, resulting in smaller pest populations and lower level of plant damage. If only some of the pest population settles, reproduction will be lower on plants connected to actuators simulating predator presence due to the ecology of fear effect. We speculate that the vibrational cues of a generalist predator will be effective in repelling/reducing populations of several crop pest species, especially if these pests and the predator share a common evolutionary background. Alternatively, a signature vibrational pattern shared by a guild of predators could impact more pest species, even in the absence of a shared evolutionary history.

The question emerges whether the predator vibrational cues can be combined with real predators for biological pest control. We hypothesize that combining the two methods will be beneficial for enhanced control of pest populations. By using predator-related vibrational cues, pests are expected to become 'confused' and less able to locate the real source of the substrate-borne vibrations, making them easier prey for real predators. As a result, we expect pest populations to be smaller when these methods are used together than when used independently. However, given that many species of predators used in biological control also use substrate-borne vibrations for prey detection, a question arises about the potential impact of using external predator vibrational cues on them. The same question is raised for the potential impact of these external predator vibrational cues on the broader arthropod community. Whether such interference occurs deserves to be investigated experimentally. A possible solution could be to avoid overlapping vibrational treatment with predator release and/or studying proper timing of applications.

### Natural enemies

We argue that previous exposure to the vibrational cues related to their target prey, reinforcing another positive experience (e.g., when food is provided) will enhance the ability of mass-reared ('naive') predators to locate their prey in the field. Thus, they will protect plants more effectively.

## Concluding remarks and future perspectives

Here, we integrate findings from biological control, the ecology of fear, and biotremology to suggest a novel theoretical framework for understanding important pending questions in plant–insect interactions and for exploring new opportunities to improve plant health and productivity. We

### Outstanding questions

Can plants distinguish between the substrate-borne vibrations generated by an antagonistic herbivore and a mutualistic predatory arthropod?

When a plant perceives substrate-borne vibrations related to the presence of a mutualistic predatory arthropod, what is the importance of other cues relative to predator presence, such as exuviae or saliva? This is particularly relevant for omnivore predators that also feed on plants, for example, predatory true bugs or phytoseiid predatory mites.

Do the substrate-borne vibrations of predatory arthropods share common characteristics that make them easily recognizable by the plants?

How do plants distinguish among the plethora of vibrations produced by herbivores, carnivores, pollinators, and abiotic factors, such as wind and rain?

What are the underlying physiological and molecular mechanisms that enable plants to selectively perceive and respond to substrate-borne vibrations?

Will plants allocate more resources to growth and reproduction when they perceive substrate-borne vibrations related to the presence of mutualistic predatory arthropods?

What is the potential impact of the vibrational cues of a predator on other arthropod predators used in augmentative biological control, as well as on the broader arthropod community?

Can pest populations adapt/habituate to the ecology of fear effect?

Can specific bee 'buzzes' trigger earlier flowering in plants?

How can substrate-borne vibrations be applied in a cost-efficient manner to improve plant protection and enhance productivity in agriculture?

argue that plants perceiving certain types of substrate-borne vibration from mutualistic arthropods, such as predators or pollinators, may allocate resources to growth or flowering, rather than to defense. Additionally, reproducing predator substrate-borne vibrations could amplify the 'ecology of fear effect', potentially reducing plant damage by repelling or slowing down the development of pest populations. Conditioning arthropod predators to the substrate-borne vibrations emitted by their target prey could increase their ability to locate and control pests in the field, leading to more efficient plant protection.

Biological control provides a very effective and sustainable option for pest control. The inclusion of the ecology of fear and biotremology can further increase the impact of biological control and potentially provide additional tools, above all, for the management of difficult-to-control pests against which the biological control options with predators and parasitoids are limited, such as the Colorado potato beetle. Our proposal offers new opportunities to study the way plants sense herbivory and their interaction with the higher trophic levels (see Outstanding questions). For example, plants respond differentially to feeding by different herbivore species, which is related to elicitors of the herbivores and associated microbes, but possibly also by different feeding modes; can this be traced back in relation to substrate-borne vibrations and induced plant defenses? Can certain substrate-borne vibrations mediate the interaction between plants and beneficial predatory arthropods or pollinators? As concerns over the impact of agriculture on the environment continue to rise, our proposal is intended to actively stimulate scientific debate among disciplines and inspire new research lines to address fundamental questions in plant–insect interactions while also promoting sustainability in agriculture.

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### Declaration of interests

A.P. is an employee of Biobest Group N.V., a private enterprise that produces and commercializes biocontrol agents for plant protection.

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