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A REVIEW ON THE POTENTIAL INTERACTION OF VIBROACOUSTIC AND ELECTROSTATIC PLANT-POLLINATOR COMMUNICATION

Ivan Sili[1*]   **Abhishek Ray Mohapatra**[1]   **Alberti Simona**[2]
Can Nerse[1]   **David Navarro-Payá**[3]   **Francesca Barbero**[2]
Gastón Pizzio[3]   **Jone Echeverria**[3]   **Lorenzo Bianco**[2]
Luca Pietro Casacci[2]   **Maria Rosaria Tucci**[3]   **Tomás Matus José**[3]
Sebastian Oberst[1]

[1] Faculty of Engineering and Information Technology, University of Technology Sydney, Ultimo NSW 2007, Australia

[2] Department of Life Sciences and Systems Biology, University of Turin, 10123, Turin, Italy

[3] Institute for Integrative Systems Biology (I2SysBio), CSIC-Universitat de Valencia, Paterna, 46908, Valencia, Spain

ABSTRACT

Pollinators, like bees, use various cues to locate flowers with rewards such as nectar and pollen. While most research focuses on olfactory and optical signals, vibroacoustic and electrostatic cues may be more critical in pollination. Studies on honeybees, bumblebees, and hoverflies indicate that the electrical charges insects accumulate assist in navigating, identifying, and potentially communicating with flowers rich in nectar or pollen. Vibroacoustic signals and cues, such as buzzing, further enhance pollen extraction. However, the interplay between vibroacoustic and electrical signals in bees, including wild bees and eusocial Australian stingless bees, remains poorly understood. Additionally, the impact of insect morphology on their ability to acquire charge through triboelectric interactions with air and plants is unclear. This study examines vibroacoustic and electrostatic communication between plants and pollinators, with a focus on analysing existing literature. We hypothesise that Australian stingless bees have evolved a mechanism like honeybees for obtaining an electrical charge, though likely smaller due to

their morphology. The review aims to facilitate the first experimental measurement of electrical charge in stingless bees.

1. INTRODUCTION

Navigation is essential for pollinators because it enables them to locate flowers efficiently, return to their nests, and ensure successful pollination, which is critical for ecosystem health and biodiversity [1]. Pollinators, including insects (bees, wasps, moths etc.), birds, and certain mammals, navigate between plants and the nest, enabling plant fertilisation through pollination between flowers. However, apart from navigation, recent research [2-5] shows that pollinators seem to communicate with the plants and make foraging decisions based on food availability and preference.

These navigation and communication mechanisms are highly diverse, encompassing a variety of sensory and cognitive strategies that allow them to find their way in complex environments. Some animals can orient themselves using the Earth's magnetic field, a process known as magnetoreception [6]. In addition to magnetoreception, animals rely on other advanced systems for navigation, such as infrasound, ultrasound, echolocation

[7] or biotremology (vibrational communication) [8]. Many insects rely heavily on their visual systems to navigate, locate food sources, and recognise landmarks [1]. Pollinators, particularly bees, see colours differently than humans. They can perceive ultraviolet (UV) light, which is invisible to the human eye. Many flowers have patterns in the UV spectrum that may enhance their attractiveness to pollinators [9].

We can classify the sensory mechanisms of communication and pollinator navigation into the following categories: olfactory, optics, vibroacoustic and electromagnetism [7]. The interaction of patterns, visual, vibrational, acoustic, and electromagnetic cues forms a complex communication network between plants and pollinators, greatly influencing the pollination process.

Communication cues are distinguishable based on their distance and timing [7] summarised in Table 1. Typically, long-distance communication occurs over a large time scale (lasting for hours), while medium- and short-distance signals are more likely to occur within minutes or seconds.

Table 1. Summary of observed common cues in the distance-time domain.

Cue Type	Distance range	Time of occurrence	Example
Olfactory	Long-range (m)	min to h	Floral scents and volatile production.
Optics	Medium-range (cm)	min	Bright colours, UV patterns.
Vibro-acoustic	Short-range (mm)	s	Buzz pollination, sugar increase to specific pollinator.
Electro-magnetism		ms	Pollen adhesion due to charge differences.

Apart from well-documented cues, researchers are investigating potential indications of an additional level of communication in plant-pollinator interactions. Recent evidence [10] indicates that the low-frequency motion of a flower (1 Hz to 2 Hz) serves as a distinct optical cue, independent of the object's shape. Experiments carried out by Desai et al. [11] suggest that foraging honeybees (*Apis mellifera*) can detect and identify both stationary and oscillating flowers, exhibiting a preference for the moving one. Further research is needed to determine whether a moving object can serve as an additional salience factor and whether pollinators use it in their decision-making.

While much research has focused on optical and olfactory cues in these interactions, the roles of vibroacoustic and electrical communication have garnered increasing interest in recent years [2-5, 12-15]. In the domain of electrical communication, publications predominantly focus on charge-measuring experiments involving honeybees [2, 16], bumblebees [17], hoverflies [5] and moths [18]. This current review aims to synthesise current knowledge regarding the significance of electrostatic fields in pollinator behaviour and plant-pollinator dynamics, as well as the potential coupling of this field with vibroacoustic cues to contribute to the field of plant-pollinator electro-acoustic (multimodal) communication.

2. ELECTROSTATIC FIELD AND CHARGE

2.1 Bee`s charge

Non-biological substances are known [19] to acquire an electric charge as they move through the atmosphere due to triboelectric charging. Experimentally observed raindrops [19] carry an electrical charge, typically ranging from 5 pico Coulombs (pC) to 100 pC, as they fall from the clouds during rainfall. With a diameter of approximately 4 mm, they are comparable in size to Australian native stingless bees, which are three to four times smaller than honeybees (Fig. 1). We assume that bees become highly triboelectrically positively charged while traveling through the atmosphere, in contrast to sessile and negatively charged flowers.

The first experiments providing some evidence of electrically charged insects were conducted in 1929 by Heuschmann [20], and bees specifically in 1975 by Erickson [21]. The last research shows that worker honeybees (*Apis mellifera*) possess a surface electrical charge when entering and leaving the hive, and the amount of the charge varies on their daily rhythm, peaking at midday or early afternoon. The experimental setup included two concentric conductive tubes with outer diameters of 12 mm and a length of 5 mm, separated by a 2 mm gap.

The calculated average charge shows that a bee returning from active flight had a charge of about 12 pC. However, due to the full contact between the bee and the tubes in this experiment and the inevitable transfer of charge while passing through the tube, the obtained results are likely lower compared to the actual value. A bee's surface can acquire and carry an electrical charge emanating a static electric field, similar to any physical object exposed to friction, pressure, or other external forces.
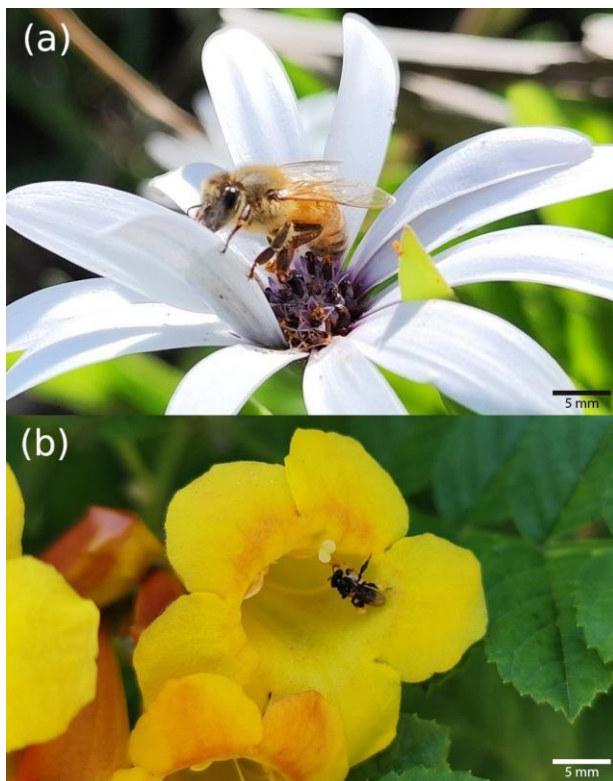
Figure 1. An equal-scale view of (a) the Western honeybee *Apis mellifera* and (b) the Australian stingless bee *Tetragonula carbonaria* foraging near local flowers in the northern region of Sydney, Australia (photo credit: Ivan Sili, November 2024)

As a result of this interaction, one entity gains additional electrons and becomes negatively charged, while the other becomes positively charged.

Over time, insects have learned to utilize the electrical charge they carry on their bodies. This charge varies based on the bee's activity, environmental conditions, and body size. There is evidence [21], that an inactive honeybee may carry a negative charge as well, typically ranging from −1.8 pC to +2.9 pC, inside the beehive at 70% humidity. An active bee, such as a dancing bee near the hive entrance, is usually positively charged up to 45 ± 4.3 pC, with a maximum charge reaching around 80 pC [21].

Colin et al. [16] measured the electrical potential of winter-clustered *Apis mellifera* and compared this to foraging bees in the spring, proposing a new technique with an induction ring. The same method and device were used in subsequent studies [17, 18]. The charge sensor consisted of two coaxial rings electrically insulated by a dielectric material. An electrometer connected to the inner ring measured the electrical current induced by the passage of a charged insect. It was observed that foraging bees typically possess smaller charges (mean = 29 ± 40 pC) than winter bees (mean = 153 ± 105 pC). Most bees carry a positive charge; however, 7% of measured bees were negatively charged, and less than 1% neutrally charged. These measurements align with findings published by Clarke et al. [22] for foraging bumblebees (mean = 32 ± 35 pC). Variations in body size among the measured bees did not significantly affect individual net charge variability, likely because fluctuations in bee size do not exceed 20%, except for the queen (whose net charge varies between +159.6 pC and +240.5 pC with a one-day delay measurement) [16]. However, the fact that the queen carries a higher amount of charge may correspond to a size-dependent charging effect, which has not been investigated yet.

Recent research by Montgomery et al. [23] suggests that the electric charge possessed by bumblebees stimulates volatile emissions. Findings indicate that *Petunia integrifolia* slightly increases the emission of behaviourally and physiologically active compounds in response to visits from positively charged bumblebees ~121 pC. Stronger emissions correlate with higher levels of electrical stimulation.

2.2 Humidity and the charge

Weather conditions, particularly relative air humidity, can significantly influence the charge carried by bees. Triboelectric charging, a primary factor in bees acquiring charge, is highly dependent on humidity levels. In [24] has shown that increasing humidity often corresponds to a decrease in bee charge, following an exponential decay relationship. The assumption is that water allows higher conductivity between two dielectric surfaces, thereby facilitating charge transfer. In conditions of high humidity, bees may have difficulty charging efficiently, which could result in reduced communication between plants and pollinators.

The only experimental study on the relationship between humidity and charging bees that we are aware of is that of Montgomery et al. [25]. The mathematical model derived as observed in the cited experiment can be represented as follows:

$$Q_{bee} = 0.26 + (5.73 - 0.022RH)\int Idt, \ [pC] \qquad (1)$$

where Q_{bee} – represents bee charge; RH – relative humidity; and I – induced electric current in the ring sensor.

Relative humidity also noticeably reduces a bee's charge retention time. An insect is likely to dissipate half of its charge within the first 30 seconds at humidity levels over 70%, while retaining 90% of its original charge when the relative humidity is below 70% [24]. Badger et al. reported [26], that a hummingbird's charge is also highly dependent on relative humidity, with net charge generally decreasing as humidity increases. Temperature, however, has no significant effect on the acquired charge. Previous research suggests that the variability of bee charges under different humidity levels should be considered when modelling future environmental experiments.

2.3 Foraging distance and the charge

One of the most common pollinators in the world, the western honeybee (*A. mellifera*), tends to visit only one type of flower while foraging in a specific direction and is highly flower-constant [27]. Bees can quickly learn all multimodal attributes of a specific plant and use this information while foraging. More than two thousand years ago, the Greek scientist Aristotle in his work "Historia Animalium" [28], remarked that a beekeeper could predict weather conditions based on the flight distance of bees. Bees can sense the approach of rain, as evidenced by their shorter flight distance. However, even under optimal weather conditions, their flight range is limited. In our current understanding, honeybee foraging range can reach up to 10 km from the hive, with a mean of 5.5 km. About 50% of bees foraged at distances more than 6 km, 25% more than 7.5 km, and only 10% more than 9.5 km [27].

Relevant work in this research line includes that of Es'kov and Sapozhnikov [29], which showed no evidence that foraging distance affects a honeybee's electric charge. Bees that flew 5 meters and 200 meters from the hive carried similar charges, varying between +0.98…+0.96 ± 0.13 pC. Controversially, in an experiment conducted by Montgomery [24], bumblebees had significantly higher charges when flying compared to walking, with positive charge increasing after more than 10 seconds of flight, assuming that flying activity impacts the positive charging of insects. This impact is expected to be logarithmic and can be approximated with:

$$Q_{bee} = 17.3 - 16.4e^{-0.17t}, \; [pC] \qquad (2)$$

where Q_{bee} - charge of the bee, and t – flight time.

Montgomery suggests [24] that a bee already carrying a positive charge is unlikely to gain additional charge during either short or long flights, emphasizing the limited electric charge saturation for an individual.

3. VIBROACOUSTICS COMMUNICATION

Vibroacoustic communication also is a crucial aspect of the interactions between pollinators, particularly bees, and flowering plants. This form of communication involves the use of vibrational and acoustic signals that can convey important information about foraging, mating, and environmental conditions.

Flight and non-flight vibrations produced by the rapid contraction of thoracic muscles in bees can be classified. To encourage bee visits, plants have evolved a mechanism to produce nectar rich in sugar and pollen, which bees collect and process to produce honey. However, certain plants, such as tomato, potato or snapdragon families, release pollen only under specific conditions, with precisely tuned vibrations being one of these requirements [12]. These vibrations are often produced by certain species of bees, known as "buzz-pollinators" [12]. This is an evolutionary adaptation that ensures more precise pollination, as only specific types of pollinators can access the pollen.

Buzz pollination is a documented yet not fully understood process employed by insects to efficiently extract pollen. The vibrations produced during buzz pollination are typically generated by the thoracic muscles through direct physical contact between the bee and the flower. During this process, a bee typically assumes a C-shaped position around the anthers and produces rapid, millisecond-long vibrations in the frequency range of 100 Hz to 400 Hz [30], often coinciding with the peak or dominant frequency, along with multiple harmonics of rapidly decreasing magnitude. This phenomenon is likely to occur in species within the families *Apidae* and *Melittidae*; meanwhile, only 6% of flowering plant species possess flowers with anthers that open in response to vibrations [31].

Bumblebees are known to transmit vibrations to flowers through various morphological structures, including the thorax, mandibles, and possibly legs [31]. Research [31] suggests that bee size is positively associated with vibration amplitude, but not necessarily with frequency. Morgan et al. [32] demonstrated that bees adjust the frequency, amplitude, and duration of their vibrations as they gain experience manipulating the same plant. Vallejo-Marín et al. [33] in their research conducted across North America, Europe, and Australia, found that the body size of bees, specifically thorax width, during non-flight defensive activity positively correlates with the acceleration amplitude of their buzzes, while it has no significant effect on buzz frequency. Non–flight (floral) vibrations exhibit also higher frequencies and greater amplitudes compared to the vibrations generated during flight. The frequency and amplitude of these vibrations play a crucial role in

determining the rate of pollen release. Observed in [34] was a positive correlation between vibration amplitude and the rate of pollen release, with a similar relationship found between higher vibration frequencies and increased pollen release and plant parts are likely grown with preferred resonance frequencies to accommodate a maximum of pollen release [35].

The most common eusocial Australian stingless bees, *T. carbonaria* and *A. australis*, have not been observed performing buzz pollination [36], likely due to their small body size. In contrast, some solitary bees, like blue-banded bees (*A. cingulata*) or carpenter bees (*Xylocopa* spp.), are recognized as native buzz pollinators in Australia [36].

While buzz-pollination is well studied, vibroacoustic signals (VAs) produced by pollinator`s wing beats could cause a potentially adaptive plant response, even before the contact between the plant and the insect. King [37] reported that after landing on a plant, the bee flaps its wings and rapidly contracts its flight muscles. The wingbeat frequency [30] of *Xylocopa* bees affects the amount of pollen removed from *Senna spectabilis*, maintaining constant values between 250 Hz and 500 Hz. In the range of 300 Hz to 400 Hz, an ejection of 0.02 to 0.10 mg of pollen was observed in flowers that received only one visit, with a tendency for less pollen to be ejected at frequencies greater than 500 Hz. The aforementioned study showed that different species of bees exhibit distinct buzzing patterns, which are related to their wingbeat frequency. Bees may modify their wingbeat frequency to approach the natural frequency of the plant they visit, optimizing the pollination process. Nerse et al. [38] studied the biomechanical properties of the snapdragon (*Antirrhinum litigiosum*) and showed how the features of flower organ material are flexible and respond to pollinator vibro-acoustic stimuli. While buzz-pollination behaviour is restricted to specific plant-insect interactions (such as those involving poricidal anthers), the responses gathered by Veits et al. [4] suggest that VA could serve as a signal potentially in all plant-insect interactions, hypothesised to be a basal plant mechanism for sensing and responding to vibrations.

4. DISCUSSION

From the analysis of the literature, we can conclude that recent research investigating the intricate communication between plants and pollinators has confirmed that electrostatic fields and vibroacoustic serve as additional cues in plant-pollinator communication.

Bees are known [39] to emanate both static and modulated electric fields. The static electric field is generated by the static charge possessed by the bee, while the modulated field is likely influenced by insect activity, with wing flapping being the most crucial factor. Although some studies have suggested this relationship [39, 40], there is no strong evidence supporting the idea that wing flapping alone modulates a bee's electric charge to a significant extent. While electrostatic interactions have been studied, the dynamic, real-time modulation of a bee's electric charge by its wing movements remains an underexplored area. Experimental research measuring both the acquired electric charge (e.g. emanating electric field) and wing flapping frequency simultaneously could provide a clearer understanding of this phenomenon.

An increase in wingbeat rate during a bee's foraging activity may enhance the positive charge it carries. Consequently, a higher charge could generate stronger electrostatic forces between the pollinator and pollen, enabling the insect to more efficiently analyse potential outcomes. Based on the measured electrical charge carried by the bees, we also aim to question whether flowers may have evolved to manipulate their electrical charges to ensure the loyalty of specific pollinators. If plants can manipulate their own electric charge in response to an approaching pollinator, this could open a new area of exploration. This trait may have evolved in a way similar to buzz pollination, but within the electrostatic realm, attracting specific pollinators to collect the pollen.

The morphology of bees determines its vibroacoustic properties. In cases where buzz-pollination is possible, the size of the thorax regulates the amplitude of the vibrations [33]. The frequency of these vibrations, however, is not influenced by body size but is instead determined by the wing flapping frequency. Additionally, bees can adjust the vibration frequency depending on the context, such as floral interaction or defensive behaviour. The potential influence of thorax size and musculature on the electrostatic charge acquired by bees, in a manner similar to their effect on vibrational properties, remains an open question. Future research is needed to investigate whether the amplitude of the electric signal, like that of vibroacoustic signals, is influenced by the size of the wing, wingspan or musculature of the thorax, clarifying the biomechanical interactions between body morphology and electrostatic charge.

A review of the literature reveals that the relationship between pollinators' morphology and their ability to acquire charge remains poorly understood. In [17] suggested that insect cuticle accumulates surface electric charge. While some evidence [14, 16] suggests that larger body size and wingspan correlate with increased charge, specific values vary among species. For instance, honeybees have been reported to possess an average charge of 29 pC [16],

bumblebees 32 pC [22], hoverflies 37 pC [5], butterflies 49 pC [18], and hummingbirds 66 pC [26]. Conversely, wasps have been reported to carry a smaller average charge of 8 pC [40], despite being larger in size compared to honeybees or bumblebees.

Why do wasps deviate from this trend? Could it be an evolutionary trait that wasps did not develop, as pollen and nectar collection are not their primary activities? Wasps have less triboelectric interaction with petals and sepals but still acquire some charge while flying through the air. Does physical contact with the flower play a more significant role in charge acquisition compared to airborne charging during flight? And what morphological features of wasps determine their small electric charge? One potential explanation is their smoother shape, with fewer body hair. In [41], researchers removed hair from the thorax of hoverflies, which reversed the polarity of the obtained charge or resulted in a neutral charge when hair from the propleuron was removed, concluded that the presence and distribution of hair on the thorax play a crucial role in determining both the amount and polarity of the induced charge. The idea that a larger surface area with longer hair could influence electric charge acquisition is also reasonable and should be further studied across different pollinator species.

But which species should be considered optimal for investigating the influence of morphological characteristics on charge acquisition? An Australian stingless bee *Tetragonula carbonaria* is a dominant candidate for such studies. These bees are approximately three to four times smaller than honeybees in terms of body size, have fewer hair on the thorax compared to honeybees or bumblebees, and possess a chitin-covered, smoother abdomen (Fig. 2a, b). We currently have no research on the average electric charge possessed by stingless bees, but considering their morphology, it could be of a lower magnitude than that of honeybees or bumblebees. The open question is whether this small charge could be sufficient for pollen adhesion via electrostatic forces. We also don't know whether stingless bees rely on vibroacoustic and electrostatic cues or both while foraging or if they prefer to use other sensory modalities or their combination. As this species deviates from *Apis* genus, they have evolved some important features to succeed in pollen and nectar collection: possession of corbiculae with hairy areas for attaching pollen grains (Fig. 2c), similar frequency of wing flapping, and, as a hypothesis, emit vibroacoustic and electrostatic stimuli to target flowers (Fig. 2d) to indicate their presence. Flowers are likely to respond to these stimuli by releasing pollen or increasing sugar concentration [4].
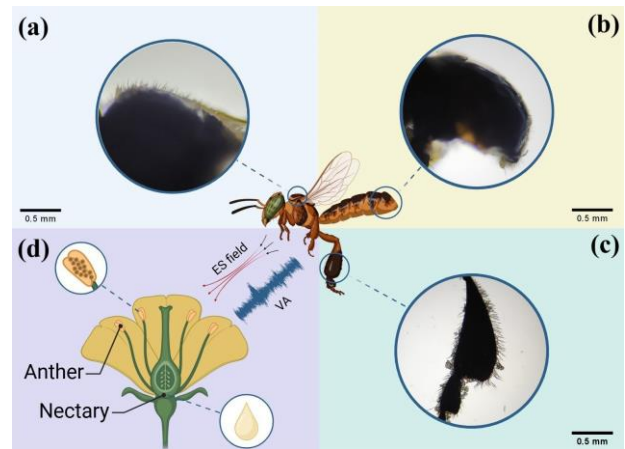

Figure 2. Morphological traits of the Australian stingless bee *Tetragonula carbonaria* and their potential impact on charge acquisition and vibroacoustic stimuli under a 40× magnification microscope view (photo credit: Ivan Sili, image created with BioRender.com). Circles indicate sampling positions on various parts of the bee's body, highlighting the detailed structure of the bee's anatomy. (a) Thorax sparsely covered with short hair. (b) Smooth hairless chitin abdomen. (c) Hairy corbicula with densely attached pollen. (d) The vibroacoustic (VA) and electrostatic (ES) stimuli emitted by a bee are hypothesized to trigger a plant's response, aiding in assessment outcomes and potentially leading to pollen release and an increase in nectar sugar concentration.

Airborne acoustic waves, thoracic vibrations, and electrostatic fields modulated by wing flapping may create a complex multimodal communication system between plants and pollinators. As a pollinator approaches a flower, it likely utilizes all available sensory modalities to evaluate the interaction and distinguish a rewarding flower. This leads to another hypothesis suggesting that a bee, upon landing a flower, may first sense the amount of pollen in the anther. Shortly after assessing the pollen, possibly through its electric charge, the "buzz bee" may either employ a vibroacoustic strategy—such as thoracic vibrations upon landing on the flower—which requires energy expenditure to obtain the reward, or choose to search for another flower that offers a more rewarding outcome without expending energy, while an increase in sugar concentration will help maintain the preferred pollinator's loyalty to the same flower.

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