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What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination

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Many plant species have evolved floral characteristics that restrict pollen access. Some of these species are visited by insects, principally bees, which make use of vibrations to extract pollen from anthers. Buzz-pollination, as this phenomenon is generally known, is a widespread method of fertilization for thousands of species in both natural and agricultural systems. Despite its prevalence in pollination systems, the ecological and evolutionary conditions that favour the evolution of buzz-pollination are poorly known. We briefly summarize the biology of buzz-pollination and review recent studies on plant and pollinator characteristics that affect pollen removal. We suggest that buzz-pollination evolves as the result of an escalation in the competition between plants and pollen-consuming floral visitors (including pollen thieves and true pollinators) to control the rate of pollen removal from flowers.

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Introduction

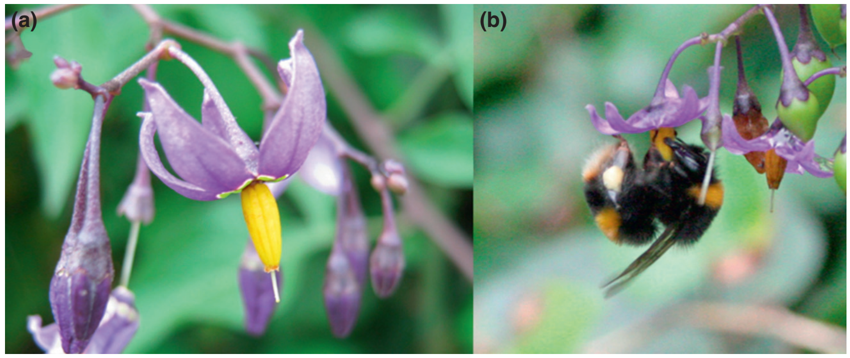
Approximately 15,000–20,000 species of plants possess flowers that release pollen only through small openings (pores or slits) in the anther's tips [1]. Insect visitors to these species resort to using vibrations — called sonications or 'buzzes' because of their audible component — to extract pollen from the anthers [1,2]. This association between restricted pollen release and the use of vibrations to remove pollen from anthers has classically been referred to as the buzz-pollination syndrome [2]. Buzz-pollinated flowers have evolved independently many times [3•], occurring in species from 65 families, including some of the world's most important agricultural crops such as tomatoes and potatoes [1,3•,4]. Among insects, the ability to sonicate is found among many species of bees (Hymenoptera: Apoidea) from seven families and more than 50 genera (but notably not honey-bees, *Apis mellifera*), and in one species of hover fly (Diptera: Syrphidae) [1,5]. Despite its widespread taxonomic distribution in plants and importance to natural and agricultural systems, buzz-pollination has received limited attention, with the last comprehensive review published exactly 30 years ago [1]. Previous work in buzz-pollination has largely focused on quantifying the biophysical properties of buzz-pollination [e.g. 2,6–8] or describing the reproductive ecology of buzz-pollinated plants [e.g. 3,9–11]. Here we provide a brief overview of the biology of buzz-pollination, discussing recent work on how plant and insect characteristics affect pollen removal, and emphasizing the ecological and evolutionary consequences of buzz-pollination for both plants and pollinators.

Morphology of buzz-pollinated flowers

Bees use vibrations to aid in pollen collection from a wide range of plant species with varied morphologies, for example, *Cistus*, *Papaver*, *Pedicularis*, Myrtaceae, and *Solanum* [3•,4,12], revealing that the vibratile release of pollen is not associated with a single type of floral morphology. However, some floral morphologies appear to have evolved specifically in response to the collection of pollen by sonicating bees [1]. The clearest example is perhaps the *Solanum*-type flower (or solanoid flower), a floral morphology that has evolved across disparate plant families, and which represents a remarkable example of convergent evolution [12–15] (Figures 1 and 2).

Solanum-type flowers illustrate many of the features characteristic of other buzz-pollinated species including releasing pollen via small apical pores or slits (i.e. poricidal anthers) [1], and often lacking nectar or other rewards to attract pollinators [12,15]. The anthers of *Solanum*-type flowers have short filaments, and are arranged centrally in a more or less closed cone [15]. The petals or sepals are free or partially united, but rarely fused in a tube, and are sometimes reflected away from the anther cone exposing the conspicuous stamens [12,15]. The pollen is concealed inside the anther which appears full even when empty. Pollen is dry, usually in single grains with smooth walls [1,12,15]. As in other species with poricidal anthers, *Solanum*-type flowers usually produce large numbers of pollen grains, and individual plants are characterised by high pollen:ovule ratios [1]. Although plants with poricidal anthers are visited by numerous insects, including beetles, flies,

Figure 1



(a) Example of a buzz-pollinated flower, *Solanum dulcamara* (Solanaceae), showing the solanoid morphology of poricidal anthers arranged in a cone at the center of the flower. **(b)** *Bombus terrestris* during a typical buzz-pollinating visit to *S. dulcamara*.

and bees, which may collect pollen by chewing or 'milking' the anthers [1,16–19], most visits are from sonicating bees [17,20].

How does buzz-pollination work?

In bees, sonication behaviours have only been reported in females, which use the collected pollen to feed developing larvae [1], and whether male bees also perform buzz-pollination is currently unknown. The behaviours exhibited by sonicating bees are fairly stereotyped [1,20]. During a typical visit, a bee lands on the flower and curls the ventral side of her body around the anthers, while grabbing their base with her mandibles (Figure 1). The bee then decouples the indirect flight mechanism to prevent wing beating and rapidly contracts its thoracic muscles. The resulting vibrations are transmitted to the anthers through the head, mandibles and ventral side of the abdomen [7,8]. The vibrations resonate in the anthers, causing pollen grains to gain energy and be expelled through the apical pores. The expelled pollen lands on the pollinator's body, perhaps being attracted by electrostatic forces [2], where it can then be groomed and collected for transport back to the hive, or carried to the stigma of another flower to complete fertilization.

The competing interests of plants and pollinators regarding pollen fate offer several interesting avenues for investigating relations between buzz-pollination vibrations and pollen release. On the one hand, the kinds of vibrations bees produce to extract pollen from anthers are expected to be shaped by morphological and behavioural aspects of individual bees. However, structural properties of stamens are also likely to influence the vibration transmission environment, but whether such plant characteristics enhance or restrict the amount of pollen released through vibration has not been thoroughly evaluated, and therefore remains a topic of some debate [6,21,22].

Properties of bee buzzes and pollen removal

The vibrations produced by sonicating bees can be characterised by three main properties: duration, frequency, and amplitude (Figure 3). Some studies suggest that pollination buzzes are identical to buzzes given in other behavioural contexts (e.g. defense or escape) [8,23•], but in fact some specific properties, such as duration and amplitude, can differ considerably (Vallejo-Marín and Cox, unpublished data; also see Supplementary Material). Vibrational properties of buzzes have been measured in only a few bee species, mainly within the genera *Bombus* and *Xylocopa* (Table 1).

Buzzes vary widely in duration both within and among species, and typically last 0.1 to a few seconds [6,7,22,24••]. Within a single buzzing sequence (Figure 3a) the number of individual pulses also varies, ranging from 1 to 17 in some *Bombus* species [7,22,24••]. When multiple pulses are produced the first two usually remove the majority of available pollen (up to 60%), with successive pulses each removing less than 10% [22]. Variability in pulse number suggests that bees adjust their behaviour to maximize pollen collection per flower while minimising buzzing effort [25]. For example, when visiting virgin flowers a bee will typically produce more buzzes per flower visit and visit longer than when visiting experimental flowers that had their pollen emptied before the bee's visit [26,27]. Furthermore, bees decrease the duration of individual pulses with successive visits to the same flower, suggesting a dynamic adjustment of behaviour in response to remaining pollen availability [28•].

The frequencies generated during buzzing vary much less than duration, principally because frequency depends on the physical and physiological properties of the vibration producing and transmitting mechanism, that is, the indirect flight muscles and exoskeleton [7,29],