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.
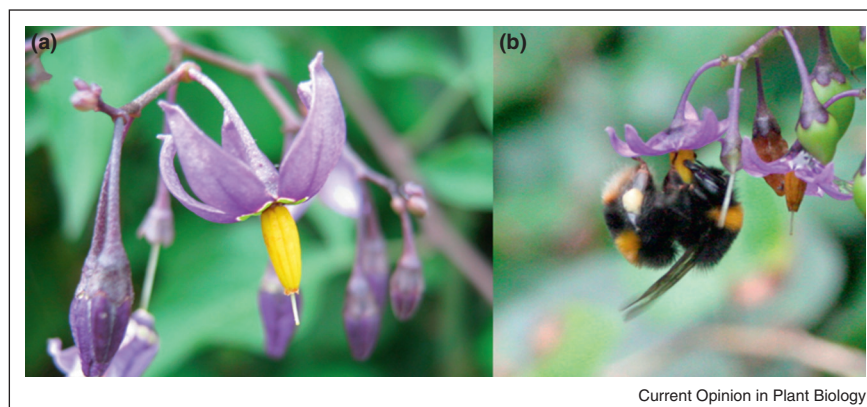
Morphology of buzz-pollinated flowers

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],

Figure 2
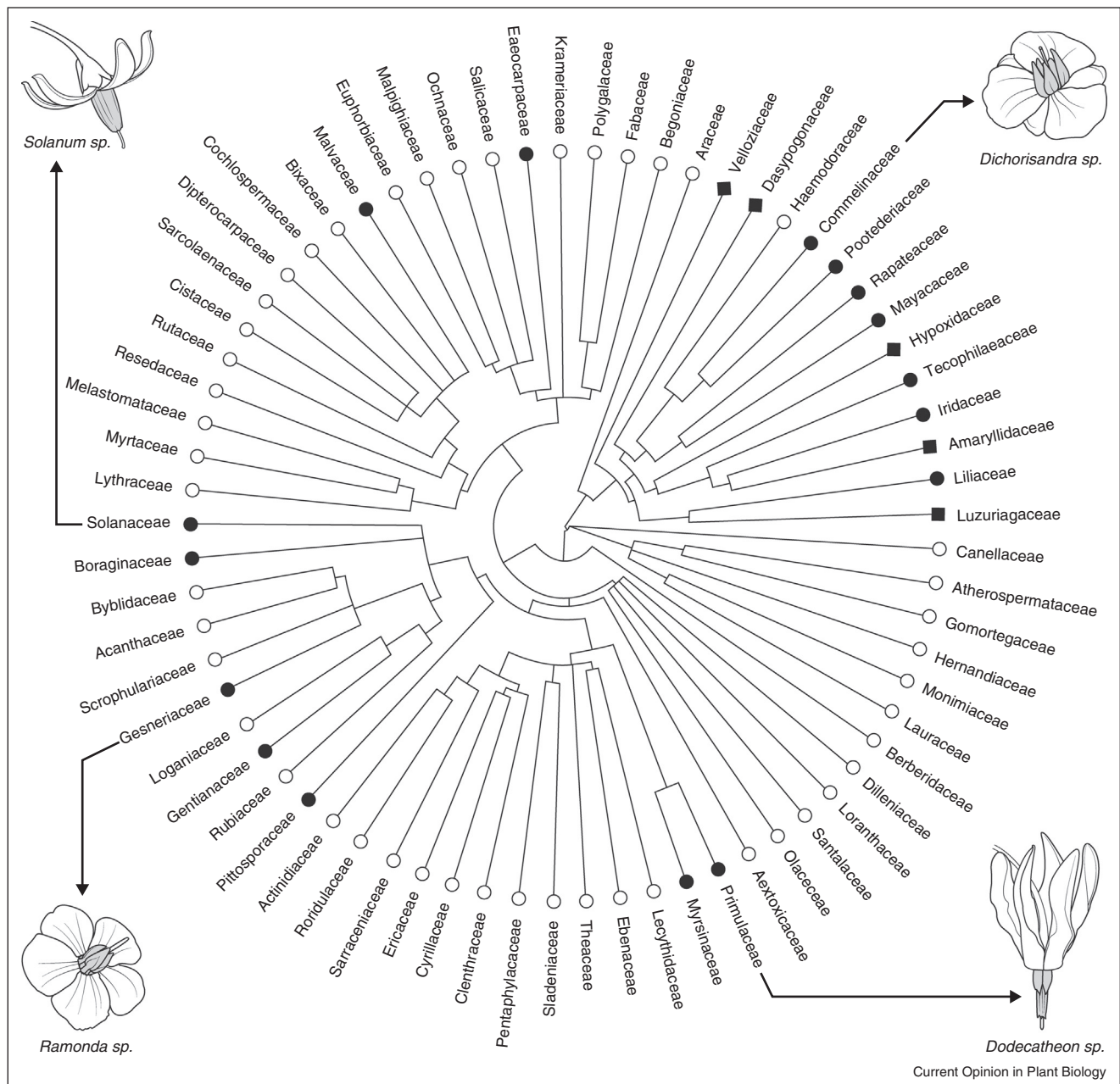
Solanum-type (solanoid) flowers have been reported in species from 21 plant families (filled symbols) across angiosperms [12,15]. For simplicity, the phylogeny shown here illustrates only those families containing at least one species with poricidal anthers (open circles), poricidal anthers and solanoid flowers (closed circles), or non-poricidal anthers and solanoid flowers (black squares). Phylogeny from Davies et al. [43]; data on poricidal anthers from Vallejo-Marín et al. [3•]. The anthers in the flower diagrams are shown in grey. Diagrams not to scale.

rather than being under behavioural control. The fundamental or peak frequency typically has the greatest energy, ranges from 100 to 400 Hz depending on the bee species (Table 1, Figure 3b), and is determined by the contraction rate of the thoracic flight muscles [29]. Harmonic frequencies (i.e. integer multiples of the fundamental frequency value caused by resonance of the vibrating exoskeleton), are usually also present and can extend up to 2000 Hz, but they contain significantly less energy than the peak frequency [7,22,24••] (Figure 3c). Because insect flight muscle has a maximum contraction rate of about 500 s^{-1} [30], bees cannot produce buzzes with higher fundamental frequencies.

The energy, or force, transmitted to a flower's anthers during a sonication bout is an integral component of

4 Biotic interactions

Figure 3
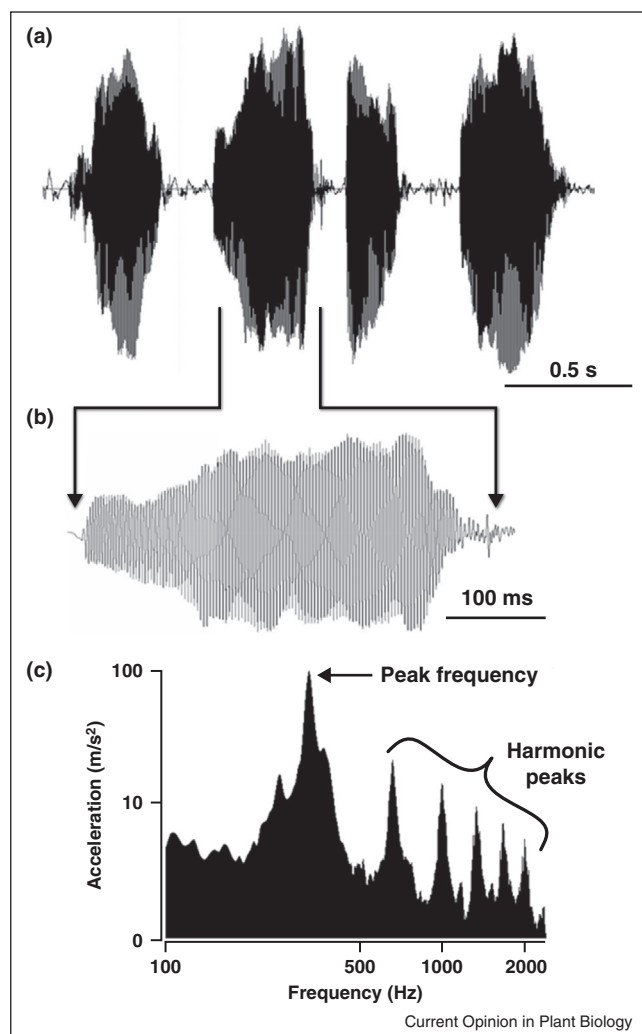
Buzz-pollination vibrations from a *Bombus terrestris* worker foraging on *Solanum rostratum*, recorded with a laser vibrometer. **(a)** Waveform of four pulses. **(b)** Expanded view of second pulse showing sinusoidal wave pattern. **(c)** Power spectrum of second buzz. The fundamental or peak frequency is approximately 330 Hz, and five harmonic frequencies are also present. Note log scale used for both axes.

offers an interesting additional function for buzzing vibrations that directly affects the fertilization success of the plant.

Few studies have quantified the effects of frequency or amplitude on the amount of pollen discharged from anthers. In *Actinidia deliciosa*, frequencies from 100 to 500 Hz are equally effective at releasing pollen [31], whereas in *Dodecatheon conjugens* more pollen is ejected at frequencies from 450 to 1000 Hz than in the 100–400 Hz range [6]. More recently, De Luca and colleagues [24••] measured natural variability in duration, frequency and amplitude of buzzes from a colony of *Bombus terrestris*, and then constructed artificial buzz stimuli varying in these parameters to explore the effect on pollen removal in *Solanum rostratum*. Pollen released from anthers increased with longer duration and greater amplitude buzzes. However, variation in frequency had a negligible effect on the amount of pollen removed.

As amplitude reflects the energy input into a buzz, it is likely to vary with the physical condition (e.g. mass, energy reserves, fatigue) of bees [7], and the ecological environment experienced during a foraging bout [32,33]. Consequently, amplitude represents an interesting parameter for further study, not only for its variability within and among species, but also because of its important role in affecting pollen ejection loads, and hence the foraging success of individual bees. For instance, in the study by De Luca and colleagues [24••] amplitude correlated positively with bee mass and greater amplitude buzzes ejected significantly more pollen in their experiment. Accordingly, larger bees foraging on buzz-pollinated flowers may enjoy the benefit of collecting more pollen per flower visited. In social species, this could have important consequences for the success of a colony since the amount of pollen returned to a nest is directly linked to the production of new workers [34].

Plant characteristics and pollen removal

Compared to studies examining buzzing vibrations produced by bees, less is known regarding the role of plant traits, in mediating vibrational properties of buzzes and pollen release. Available studies indicate that floral structures such as anther filaments can enhance or dampen the amplitude of vibrations produced by bees and potentially affect pollen ejection [2,6,21]. In particular, strong damping will absorb vibration energy, reducing the anther (and pollen) resonation at certain frequencies. For example, the anthers of *Solanum laciniatum* have low damping coefficients that likely assist the transmission of vibrations, and are also lower than for *Rhododendron* sp. anthers, which are not buzz-pollinated [21,22]. A species-specific relation between pollen removal by vibrations and stamen characteristics is suggested by comparison of several *Solanum* species, which showed that the number of artificial vibrations applied to anthers to empty them of pollen varies

buzzing. In this review we use peak amplitude to refer to the energy contained within a buzzing vibration, and for uniformity among studies we express peak amplitude in acceleration units (m/s^2). Bees produce sufficiently high accelerations at peak frequencies to adequately expel pollen, although there is large variability among individual bees and among species [7,24••]. Because harmonics contain significantly less energy than peak frequencies they are thought to contribute little, if any, to pollen ejection [22]. However, Arceo-Gómez and colleagues [23•] recently suggested that once pollen is expelled from anthers, harmonic frequencies above 1000 Hz may aid in pollen capture and deposition on stigmas. This finding

Table 1

Bee and flower species for which pollination buzzes have been measured. Body length ranges were obtained from measurements provided in the literature or from online sources. Peak frequency refers to the frequency with the greatest relative energy within a buzzing vibration ('–' value not reported, 'n/a' not applicable).

Bee species	Body length range (mm)	Peak frequency range (Hz)	Peak amplitude range (m/s^2)	Plant species used to record buzzes from	Source
Bombus terrestris L.	11–17	300–385	142–212	*Actinidia deliciosa, Borago officinale, Solanum laciniatum, S. rostratum, Symphytum officinalis*	[31,7,22,8,24$^{\bullet\bullet}$]
B. pratorum L.	10–14	225–280	–	*B. officinale, S. officinalis*	[31]
B. pascuorum Scopoli	10–15	280	–	*B. officinale, S. officinalis*	[31]
B. hortorum L.	11–16	323–385	199	*S. officinalis*	[31,7]
B. bifarus Cresson	16	315–327	–	*Dodecatheon conjugens*	[6]
B. melanopygus Nylander	16	315–327	–	*D. conjugens*	[6]
B. occidentalis Greene	9–14	253–371	64	*D. conjugens*	[6,29,8]
Xylocopa californica Cresson	25–28	197–297	–	n/a	[29]
X. c. arizonensis Cresson	25–28	174–346	105–109	n/a	[8]
X. varipuncta Patton	25	117–288	61	n/a	[29,8]

significantly among species with different anther structural properties (i.e. more pollen is released from multi-layered and rigid anthers vs. single-layered and flexible anthers) [35]. The size of the anther pore relative to pollen diameter may also regulate pollen release in response to vibrations [20]. An interesting avenue for further research concerns whether anthers are frequency-tuned, that is, dispense more pollen at certain frequencies than others, which some researchers argue functions as a dispensing mechanism by plants to restrict exploitation of pollen resources by soni-cating bees [(6, but see 22)]. Unfortunately, we currently lack sufficient empirical data regarding inter-species variability in frequency response characteristics of anthers, and such information is vital to evaluate potential co-evolutionary dynamics (e.g. cooperation vs. conflict) that might exist between buzz-pollinated plants and pollinators that use vibrations to extract pollen. Further experimental and comparative studies of functional relations between stamen traits, buzzing vibrations and pollen release are therefore needed.

Evolutionary significance of buzz-pollination
The evolution of buzz-pollination was likely triggered by the necessity of nectarless plants to restrict pollen access, reducing gamete loss to inefficient pollinators and pollen thieves, that is, visitors that remove pollen with little or no contribution to deposition on stigmas [36$^{\bullet\bullet}$], and maximizing pollen dispersal to conspecific plants [6,37]. Nectarless flowers are prone to particularly high rates of pollen loss as they are visited by bees, which are effective in removing large amounts of pollen [1,12]. Poricidal anthers may exclude some visitors (pollen eating beetles, flies, and non-buzzing bees), and could also act as a pollen-dispensing mechanism to maximize pollen export by legitimate buzz-pollinators [6,22,38,39] (Figure S1a). In animal-pollinated plants, pollen removal during a single visit usually has decelerating effects on the probability of successfully

fertilizing ovules [39]. Poricidal anthers may also help to increase the efficiency of pollen transfer by ejecting pollen onto specific areas of the pollinator's body where it is less likely to be groomed, that is, in 'safe sites' [40], or more likely to contact the stigma of other flowers [6,10].

The evolution of poricidally dehiscent anthers probably had a significant impact on the ability of different types of pollinators to remove pollen (Figure S1b). Non-buzzing visitors, such as flies and some bees, are limited to extracting small amounts of pollen from such anthers by gleaning it from the anther pores or by inserting their mouthparts into them [36$^{\bullet\bullet}$]. Furthermore, some beetles and bees (*Trigona* spp.) that chew their way into the anther sacs probably expend considerable time before reaching the pollen inside. By contrast, buzzing bees can quickly extract a large proportion of pollen from poricidal anthers [18,40]. These differences in pollen removal efficiency are probably the reason why buzz-pollinated plants are mainly visited by sonicating bees, that is, they are 'functionally specialised' [17,20].

Given that bees produce buzzes in many contexts (e.g. defense, compacting sand, and to warm a nest) [1], it is surprising that some pollen-collecting bees such as *Apis mellifera* (honey-bees) and *Trigona* spp., visiting buzz-pollinated flowers seem incapable of sonication [1,8,25]. Buzz-pollination is probably an innate behaviour in some species, as naive *Bombus terrestris* bumblebees foraging on buzz-pollinated flowers will exhibit buzzing on their first foraging trips [7]. However, a learned component almost certainly exists as well, as *B. terrestris* workers improve their buzz-pollination technique during several days of repeated foraging [41]. Establishing the factors that allowed the evolutionary incorporation of vibrations into pollen collection in some bee species, but not others, will certainly require

comparative analyses of physiological, behavioural and ecological characteristics.

The close interaction between buzz-pollinated plants and their pollinators has given rise to remarkable examples of convergent evolution and co-adaptations. In some cases, plants from unrelated families have evolved typified floral morphologies as a response to selection from their buzz-pollinators [1,12,14] (Figure 2). In others, different floral structures have been recruited to restrict pollen access (e.g. poricidal anthers in most buzz-pollinated plants vs. closed staminate flowers in *Dalechampia* sp. blossoms [42••]). The close physical contact required between pollinator and flower may also have facilitated the evolution of complex adaptations, an example of which is the functional specialisation of stamens of some buzz-pollinated species into feeding and pollinating functions, that is, heteranthery [3•,9,10].

Conclusions and future prospects

Buzz-pollination is a phenomenon where many basic questions remain unanswered. On the bee side, we need more data on additional species describing variability in buzzing vibrations (see Supplementary Material for recommendations on recording procedures). On the plant side, we need more information from more species about floral characteristics most important for mediating the effect of vibrations on pollen removal. Clearly, distinguishing the innate and learned components of buzz-pollination and the extent to which individual bees can adjust their vibrations to specific plant species could have important practical implications for pollination services in both natural and agricultural systems. A difficult but fundamental challenge will be to evaluate the fitness consequences of different patterns of pollen removal and collection for both plants and pollinators. Understanding these fitness consequences will allow refining and testing evolutionary hypotheses, clarifying the role of pollen loss as an important selective pressure favouring the evolution of buzz-pollination. Buzz-pollination studies would particularly benefit from collaborative work between plant and insect biologists, and from explicitly combining knowledge of biophysics, physiology, genetics, behaviour, ecology, and evolution. Integration among these subjects will be crucial to develop a thorough understanding of the factors that have shaped and continue to influence this fascinating biotic interaction.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pbi.2013.05.002.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

• of special interest
•• of outstanding interest

1. Buchmann SL: **Buzz pollination in angiosperms**. In *Handbook of Experimental Pollination Biology.* Edited by Jones CE, Little RJ. van Nostrand Reinhold Company, Inc.; 1983:73-113.

2. Buchmann SL, Hurley JP: **Biophysical model for buzz pollination in Angiosperms**. *J Theor Biol* 1978, **72**:639-657.

3. Vallejo-Marín M, Da Silva EM, Sargent RD, Barrett SCH: **Trait correlates and functional signficance of heteranthery in flowering plants**. *New Phytol* 2010, **188**:418-425.
• A phylogenetic analysis across flowering plants that reveals a strong association between poricidal anthers, nectarless flowers and anther dimorphism.

4. Proenca CEB: **Buzz pollination: older and more widespread than we think?** *J Trop Ecol* 1992, **8**:115-120.

5. Thorp RW: **The collection of pollen by bees**. *Plant Syst Evol* 2000, **222**:211-223.

6. Harder LD, Barclay MR: **The functional significance of poricial anthers and buzz pollination: controlled pollen removal from *Dodecatheon***. *Funct Ecol* 1994, **8**:509-517.

7. King MJ: **Buzz foraging mechanism in bumble bees**. *J Apicultural Res* 1993, **32**:41-49.

8. King MJ, Buchmann SL: **Floral sonication by bees: mesosomal vibration by *Bombus* and *Xylocopa,* but not *Apis* (Hymenoptera: Apidae), ejects pollen from poricidal anthers**. *J Kansas Entomol Soc* 2003, **76**:295-305.

9. Luo Z, Zhang D, Renner SS: **Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis**. *Funct Ecol* 2008, **22**:794-800.

10. Vallejo-Marín M, Manson JS, Thomson JD, Barrett SCH: **Division of labour within flowers: heteranthery, a floral strategy to reconcile contrasting pollen fates**. *J Evol Biol* 2009, **22**:828-839.

11. Larson BM, Barrett SCH: **The pollination ecology of buzz-pollinated *Rhexia virginica* (Melastomataceae)**. *Am J Bot* 1999, **86**:502-511.

12. Vogel S: **Evolutionary shifts from reward to deception in pollen flowers**. In *The Pollination of Flowers by Insects.* Edited by Richards AJ. Academic Press; 1978:89-96.

13. Mast AR, Feller DMS, Kelso S, Conti E: **Buzz-pollinated *Dodecatheon* originated from within the heterostylous *Primula* subgenus *auriculastrum* (Primulaceae): a seven-region cpDNA phylogeny and its implications for floral evolution**. *Am J Bot* 2004, **91**:926-942.

14. Barrett SCH: **Darwin's legacy: The forms, function and sexual diversity of flowers**. *Philos Trans R Soc Lond B* 2010, **365**:351-368.

15. Faegri K: **The solanoid flower**. *Trans Botanical Soc Edinburgh* 1986, **45(S1)**:51-59.

16. Thorp RW, Estes JR: **Intrafloral behavior of bees on flowers of *Cassia fasciculata***. *J Kansas Entomol Soc* 1975, **48**:175-184.

17. Larson BM, Barrett SCH: **The ecology of pollen limitation in buzz-pollinated *Rhexia virginica* (Melastomataceae)**. *J Ecol* 1999, **87**:371-381.

18. Renner SS: **The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae**. *Biotropica* 1983, **15**: 251-256.

19. Renner SS: **A survey of reproductive biology in Neotropical *Melastomataceae* and *Memecylaceae***. *Ann Missouri Bot Gard* 1989, **76**:496-518.

20. Macior LW: **Experimental study of floral ecology of *Dodecatheon meadia***. *Am J Bot* 1964, **51**:96-108.

21. King MJ, Buchmann SL: **Bumble bee-initiated vibration release mechanism of *Rhododendron* pollen**. *Am J Bot* 1995, **82**: 1407-1411.

22. King MJ, Buchmann SL: **Sonication dispensing of pollen from *Solanum laciniatum* flowers**. *Funct Ecol* 1996, **10**:449-456.

23. Arceo-Gómez G, Martinez ML, Parra-Tabla V, Garca-Franco JG:
• **Anther and stigma morphology in mirror-image flowers of *Chamaecrista chamaecristoides* (Fabaceae): implications for buzz pollination**. *Plant Biol* 2011, **13(Suppl 1)**:19-24.
This study offers a novel additional function for the frequency component of buzzing vibrations that directly affects plant fertilization success by facilitating the capture of pollen by stigmas.

24. De Luca PA, Bussiere LF, Souto-Vilaros D, Goulson D, Mason AC,
•• Vallejo-Marin M: **Variability in bumblebee pollination buzzes affects the quantity of pollen released from flowers**. *Oecologia* 2013 http://dx.doi.org/10.1007/s00442-012-2535-1.
This is the first study to test the simultaneous influence of multiple buzzing parameters on the magnitude of pollen release, including an evaluation of interactions between buzzing properties that also influence pollen ejection dynamics.

25. Buchmann SL, Cane JH: **Bees assess pollen returns while sonicating *Solanum* flowers**. *Oecologia* 1989, **81**:289-294.

26. Cane JH, Buchmann SL: **Novel pollen-harvesting behavior by the bee *Protandrena mexicanorum* (Hymenoptera, Andrenidae)**. *J Insect Behav* 1989, **2**:431-436.

27. Harder LD: **Behavioral responses by bumble bees to variation in pollen availability**. *Oecologia* 1990, **85**:41-47.

28. Kawai Y, Kudo G: **Effectiveness of buzz pollination in
• *Pedicularis chamissonis*: significance of multiple visits by bumblebees**. *Ecol Res* 2009, **24**:215-223.
A demonstration of how individual bees adjust specific aspects of sonication behaviour while foraging in response to remaining pollen loads in anthers.

29. King MJ, Buchmann SL, Spangler HG: **Activity of asynchronous flight muscle from two bee families during sonication (buzzing)**. *J Exp Biol* 1996, **199**:2317-2321.

30. Marden JH: **Variability in the size, composition, and function of insect flight muscles**. *Annu Rev Physiol* 2000, **62**:157-178.

31. Corbet SA, Chapman H, Saville N: **Vibratory pollen collection and flower form: bumble-bees on *Actinidia*, *Symphytum*, *Borago* and *Polygonatum***. *Funct Ecol* 1988, **2**:147-155.

32. Rasheed SA, Harder LD: **Foraging currencies for non-energetic resources: pollen collection by bumblebees**. *Anim Behav* 1997, **54**:911-926.

33. Peat J, Goulson D: **Effects of experience and weather on foraging efficiency and pollen versus nectar collection in the bumblebee, *Bombus terrestris***. *Behav Ecol Sociobiol* 2005, **58**:152-156.

34. Heinrich B: *Bumblebee Economics*. Cambridge: Harvard Universtiy Press; 1979, .

35. Passarelli L, Cocucci A: **Dynamics of pollen release in relation to anther-wall structure among species of *Solanum* (Solanaceae)**. *Aust J Bot* 2006, **54**:765-771.

36. Hargreaves AL, Harder LD, Johnson SD: **Consumptive
•• emasculation: the ecological and evolutionary consequences of pollen theft**. *Biol Rev* 2009, **84**:259-276.
A comprehensive review on pollen consumption that highlights the importance of pollen theft, which is an often neglected component of plant–pollinator interactions.

37. Harder LD, Wilson WG: **Theoretical perspectives on pollination**. *Acta Hortic* 1997, **437**:83-101.

38. Harder LD, Thomson JD: **Evolutionary options for maximizing pollen dispersal of animal-pollinated plants**. *Am Natural* 1989, **133**:323-344.

39. Harder LD, Wilson WG: **Theoretical consequences of heterogeneous transport conditions for pollen dispersal by animals**. *Ecology* 1998, **79**:2789-2807.

40. Buchmann SL: **Bees use vibration to aid pollen collection from non-poricidal flowers**. *J Kansas Entomol Soc* 1985, **58**:517-525.

41. Laverty TM: **The flower-visiting behaviour of bumble bees: floral complexity and learning**. *Can J Zool* 1980, **58**:1324-1335.

42. Armbruster WS, Lee J, Edwards ME, Baldwin BG: **Floral
•• paedomorphy leads to secondary specialization in pollination of Madagascar Dalechampia (Euphorbiaceae)**. *Evolution* 2013, **67**:1196-1203.
The first record in Euphorbiaceae of an adaptation in inflorescence morphology in response to sonicating pollinators. It shows a striking example of evolutionary convergence to a buzz-pollinated flower morphology by modification of staminate flowers rather than individual anthers.

43. Davies TJ, Barraclough TG, Chase MW, Soltis PS, Soltis DE, Savolainen V: **Darwin's abominable mystery: insights from a supertree of the angiosperms**. *Proc Natl Acad Sci* 2004, **101**:1904-1909.