

Buzz pollination: A theoretical analysis via scaling invarianceDaniel Borin ¹, Vinicius Lourenço Garcia de Brito ², Edson Denis Leonel ¹ and Matheus Hansen ³¹*São Paulo State University (UNESP), IGCE - Physics Department, 13506-900, Rio Claro, SP, Brazil*²*Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, 38405-315, MG, Brazil*³*Center for Mathematics and Applications (NOVA Math), NOVA School of Science and Technology (NOVA FCT), Universidade NOVA de Lisboa, Quinta da Torre, 2829-516, Caparica, Portugal*

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Nearly half of the bee species can perform a fascinating stereotyped behavior to collect pollen grains by vibrating flowers, known as buzz pollination. During the floral visit, these bees mechanically transfer the vibrations produced by their thoracic indirect flight muscles to the flower anther, inducing the movement of the pollen grains and leading them to be released through a small pore or slit placed at the tip of the anther in poricidal flowers. In such flowers, pollen release is affected by the vibrational behavior of buzzing bees, primarily their duration and velocity amplitude. However, we know little about how poricidal anther morphology may influence it. In this work, we investigated through a theoretical and numerical point of view the buzz pollination process considering a typical poricidal anther of a tomato flower (*Solanum lycopersicum*), which in our work will be approached by a rectangular billiard, experiencing vibrations applied by a bumblebee (*Bombus terrestris*). Our primary goals in this paper are (i) to understand the mechanism behind the pollen release in this model, (ii) to observe some scale effects associated with morphological variations of the anther (as pore size and anther shape), and (iii) analyze how these results are related to natural buzz pollination systems.

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Animal vectors pollinate most flowering plants, making bees the most frequent pollinator group [1–3], it being estimated that bees are responsible for nearly 80% of all insect-mediated pollination in nature [4–6]. During their floral visits, bees can perform several behaviors to collect different floral resources such as nectar, oils, and pollen grains. A fascinating case of such bee behavior on flowers is floral buzzing [7,8]. Medium to large-sized female bees of many species can vibrate their thoracic muscles on flowers to collect pollen grains [9]. Such high-pitched vibrations are mechanically transferred to anthers, releasing pollen, which is eventually deposited onto stigmas in a process called buzz pollination [8,10,11]. Buzz pollination may occur in more than 20 000 flowering species, distributed in 65 nonrelated families, most of them bearing tubular anthers that open by a small apical pore or slit and provide pollen as the only or leading floral resource, the so-called “pollen flowers” [10,12]. Although buzz pollination is a well-documented phenomenon, the mechanical interaction of poricidal anthers with bee mechanical vibrations and its effect on pollen release is still poorly understood.

The vibrations of thoracic muscles are part of several bee behaviors, including flight, thermogenesis, communication, and buzz pollination. In general, while visiting flowers, bees may produce continuous vibrations of up to two seconds or several multiple short pulses of vibrations of tens to hundreds of milliseconds [8,13]. Such mechanical floral vibrations have a high fundamental peak frequency (i.e., number of cycles per second), generally from 100 Hz to 400 Hz. Finally, the bee’s vibrations may also be described by the amplitude (i.e., the magnitude of change of sinusoidal motion) of their body

displacement, velocity, or acceleration. Despite amplitude being hard to measure during floral buzzing empirically, it is believed to be, together with vibration duration, the most crucial bee vibrational component related to pollen released by poricidal anthers. When all the other vibrational parts are kept constant, peak velocity amplitude is the most promising observable affecting pollen release by poricidal anthers in numerical approaches [14]. Besides the biomechanical abilities of bees during floral buzzing, the anther morphology should also play a key role in pollen release during buzz pollination [15].

There is a vast morphological diversity of poricidal anthers in buzz-pollinated pollen flowers. Poricidal anthers may vary in shape, size, and pore size among species and even within species in the same flower (i.e., heteranthery). These anther morphological traits may affect pollen release during floral buzzing. More prominent anthers release more pollen grains per time unit than small ones during flower lifespan [15]. However, given the reduced spatial scale of such a phenomenon, it is hard to access the physical features of individual pollen grains, as the escape probability from the anther, which can hamper our understanding of other potential effects of anther morphology in pollen release. In this sense, mathematical models describe it better and create theoretical hypotheses that could be empirically tested.

In this study, we are particularly interested in investigating the buzz pollination process considering a billiard approach [16–18]. Our method considers the anther of the flower shaped as a billiard system, which has a boundary that will oscillate according to specific vibrations produced by a bee to simulate a typical buzz pollination process [14]. In this way, we simulate the contact between a tomato flower (*Solanum*



FIG. 1. (a) *Solanum lycopersicum* flower, and (b) a bumblebee (*Bombus terrestris*).

lycopersicum) and a bumblebee (*Bombus terrestris*), as illustrated in Fig. 1.

The main goal is to connect the probability of particles' escape in open systems and concepts of scale invariance with morphological traits of the anther and observe how this may influence the amount of pollen released. Our findings contribute to linking traditional concepts about escaping particles in dynamical systems with current discussions about the main factors involved in pollen release by poricidal anthers under bee vibration.

This paper is organized as follows. In Sec. II, we present all the considerations about our model and how it can be related to the buzz pollination process. Section III is dedicated to the numerical results, as well as its appropriate discussion, and lastly, in Sec. IV, we present our final remarks, conclusions, and perspectives for future works.

II. BILLIARD APPROACH

An anther is the male floral reproductive organ in which the sporogenic tissue develops, subsequently creating and storing the pollen grains. In this work, we are engaging in a particular type of anther, known as poricidal [11, 19], in which the pollen release occurs when pollen grains escape through a small apical pore or slit located on its tip. This type of anther occurs

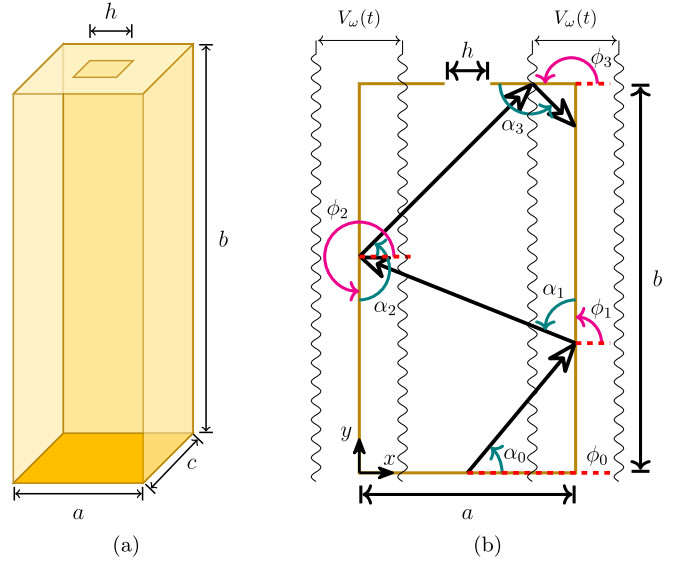


FIG. 2. (a) Illustration of the box-shaped poricidal anther, as proposed by Buchmann and Hurley [20], and (b) The rectangular two-dimensional billiard approach for the poricidal anther model.

in about 6% of flowering plants, including some very familiar crops, such as the tomato flower [10]. In 1978, Buchmann and Hurley [20] proposed a model to shape a poricidal anther to study the buzz pollination process of tomato flowers, considering the anther with a geometrylike box shape, as illustrated in Fig. 2(a). Typically, for these anthers, the dimensions of the box are $a = 0.69$ mm, $b = 5.07$ mm, and $c = 0.69$ mm, while the size of the pore is $h = 0.22$ mm [21]. Since both dimensions a and c are small when compared to b , we can neglect the plan c and consider the dynamics of the system in a two-dimensional plan [14], as displayed in Fig. 2(b). In this way, a traditional two-dimensional billiard system can describe the morphology of the poricidal anther discussed above.

To simulate the vibrations produced by a bumblebee in our dynamical system, we considered some recent experimental and theoretical investigations [8, 14] in which these vibrations might be approximately describe by the functions

$$\begin{aligned} S_\omega(t) &= \eta[\cos(\omega_1 t) + \cos(\omega_2 t)], \\ V_\omega(t) &= -\eta[\omega_1 \sin(\omega_1 t) + \omega_2 \sin(\omega_2 t)], \\ a_\omega(t) &= \eta[\omega_1^2 \cos(\omega_1 t) + \omega_2^2 \cos(\omega_2 t)], \end{aligned} \quad (1)$$

where $S_\omega(t)$, $V_\omega(t)$, and $a_\omega(t)$ are the displacement, velocity, and acceleration of the anther vibration, respectively, considering $\eta = 1$ μm as the half of the amplitude displacement of vibration, $\omega_1 = 2513.27$ rad/s and $\omega_2 = 2450.44$ rad/s being the angular frequency of the waves, and t the time measures in seconds. These parameter values are chosen to accurately reproduce the experimental data on the acceleration vibrations experienced by the anthers when a *B. terrestris* visits a buzz-pollinated flower, as reported in Vallejo-Marín's work [8].

As shown in Fig. 2(b), the particle's trajectory is influenced by the angle α_n (measured between the particle's path and a tangent line at the billiards's boundary) and its velocity V_n . In this context, the subscript n denotes n th collision of the pollen with the border.

Our description will not consider the gravitational force since the floral orientation does not affect the amount of pollen released for *Solanum* species [22]. Besides, considering that the amplitude of a_ω (for the parameters above) assumes a value next to gravitation acceleration, we can consider that these effects cancel each other out. Therefore, without external forces within the anther, the pollen exhibits a free motion (straight-line trajectory) between each collision. Considering rectangular coordinates, we can define the evolution of pollen grain position inside the anther as

$$\begin{aligned} x_p(t) &= x_n + |\vec{V}_n| \cos(\alpha_n + \phi_n)[t - t_n], \\ y_p(t) &= y_n + |\vec{V}_n| \sin(\alpha_n + \phi_n)[t - t_n], \end{aligned} \quad (2)$$

where

$$\phi_n = \begin{cases} 0, & y_n = 0 \text{ (base boundary),} \\ \frac{\pi}{2}, & x_n = a \text{ (right boundary),} \\ \pi, & y_n = b \text{ (top boundary),} \\ \frac{3\pi}{2}, & x_n = 0 \text{ (left boundary).} \end{cases}$$

Note that ϕ_n has its values always based on the last position of the particle at the boundary of the billiard (x_n, y_n) .

As an initial approach, we assumed that the vibration produced by the bumblebee affects only the vertical walls of the billiard, resulting in a velocity of type

$$\vec{V}_w = -V_w(t) \sin(\phi_n) \hat{i}, \quad (3)$$

where $V_w(t)$ is given by Eq. (1). We can assume this because, although bees produce vibrations in all three dimensions, the force vibrations produced along the y axis (corresponding to the vertical walls in our system) are 150–250% higher than the force applied in the other dimensions [23]. Additionally, the same anther axis is more prone to vibrate than the others [24].

Naturally, if $\vec{V}_w \neq 0$, the velocity of pollen grains can increase or decrease depending on the instant of collision with the boundary. The momentum conservation law gives the reflection rules of the system,

$$\vec{V}_{n+1} \cdot \vec{T}_{n+1} = (1 - \xi) \vec{V}_{w_{n+1}} \cdot \vec{T}_{n+1} + \xi \vec{V}_n \cdot \vec{T}_{n+1}, \quad (4)$$

$$\vec{V}_{n+1} \cdot \vec{N}_{n+1} = (1 + \kappa) \vec{V}_{w_{n+1}} \cdot \vec{N}_{n+1} - \kappa \vec{V}_n \cdot \vec{N}_{n+1}, \quad (5)$$

where $\vec{T}_{n+1} = \cos(\phi_{n+1}) \hat{i} + \sin(\phi_{n+1}) \hat{j}$, $\vec{N}_{n+1} = -\sin(\phi_{n+1}) \hat{i} + \cos(\phi_{n+1}) \hat{j}$ are the tangent and normal unit vectors, and $\vec{V}_{w_{n+1}}$ is the velocity of the boundary, at collision $n + 1$. The coefficients $\xi, \kappa \in [0, 1]$ are the restitution parameters for collision along the tangent and normal directions, respectively, which in our simulations will be assumed to be equal to one once all the collisions are elastic.

Through Eqs. (4) and (5), we obtain the velocity of the pollen grain after the collision $n + 1$ with the boundary as

$$|\vec{V}_{n+1}| = \sqrt{[\vec{V}_{n+1} \cdot \vec{T}_{n+1}]^2 + [\vec{V}_{n+1} \cdot \vec{N}_{n+1}]^2},$$

where the reflection angle α_{n+1} is given by

$$\alpha_{n+1} = \arctan \left[\frac{\vec{V}_{n+1} \cdot \vec{N}_{n+1}}{\vec{V}_{n+1} \cdot \vec{T}_{n+1}} \right].$$

III. SCALING INVARIANCE ANALYSIS

Scaling invariance is a concept that permeates various domains of science and mathematics once it explores the possibility that particular phenomena may remain unchanged under the rescaling or transformation of its parameters. In other words, if a system presents scaling invariance, then independently of its scale, the expected behaviors remain consistent, providing valuable insights into the underlying structure, something highly desirable, especially when dealing with complex systems. This characterization can be seen in several systems as diffusive process [25], social network [26], fractional [27], and chaotic dynamics [28].

Our primary goal in this section is to study the pollen release considering the rectangular billiard proposed in the previous section. However, besides observing the behavior of the escape probability associated with the number of pollen grains that leave the anther during such an analysis, we are particularly interested in observing if such behavior might exhibit standardlike or scale-invariant characteristics for some geometric alterations of the billiard, which, without loss of generality, might be linked to poricidal anthers. In nature, poricidal anthers present drastic scale variations from species to species or even within the same species. For example, the anther length in *Solanum citrifolium* is more than threefold higher than in its sister species *Solanum heterodoxum* [29]. In *Pleroma raddianum* (*Melastomataceae*), another buzz-pollinated poricidal anthered species, the anther length of pollination stamens is 30% higher than the length of feeding stamens within the same flower [15]. In this work, we considered the variation in the size of the pores as well as in the geometry of poricidal anthers.

We start a numerical analysis defining the escape probability $P_E(t)$. This cumulative distribution refers to the possibility of observing particles (pollen grain in our model) being released from the billiard after $n(t)$ collisions with the boundary. Numerically, this measure is computed as

$$P_E(t) = \frac{1}{M} \sum_{j=1}^{n(t)} H_M(j), \quad \text{for } n(t) \in \mathbb{N} \text{ and } t < T, \quad (6)$$

where $H_M(j)$ denotes the histogram associated with M distinct particles, which are released until j collisions and t is the mean time after n impacts with the boundary. To calculate $H_M(j)$, we consider an ensemble of M distinct and noninteracting initial conditions (pollen grains in the model) inside the billiard and evolve each one in the system. When the pollen grain reaches the pore (represented as a hole in our model), we record the number of collisions up to that moment and subsequently initialize a new particle in the system. Such a procedure is repeated multiple times until all the initial conditions have been exhausted. Here, it is important to mention that in our approach, each particle has a maximum evolution time of $T = 2.25$ seconds within the system. This time interval is within the range of buzz durations performed by *B. terrestris* in *Solanum rostratum* flowers [30].

Pollen grains in angiosperms can be very small, often only a few microns in size. For instance, pollen from tomato flowers, which are pollinated by pollen-foraging bees, is notably smaller compared to pollen from other plants [31].

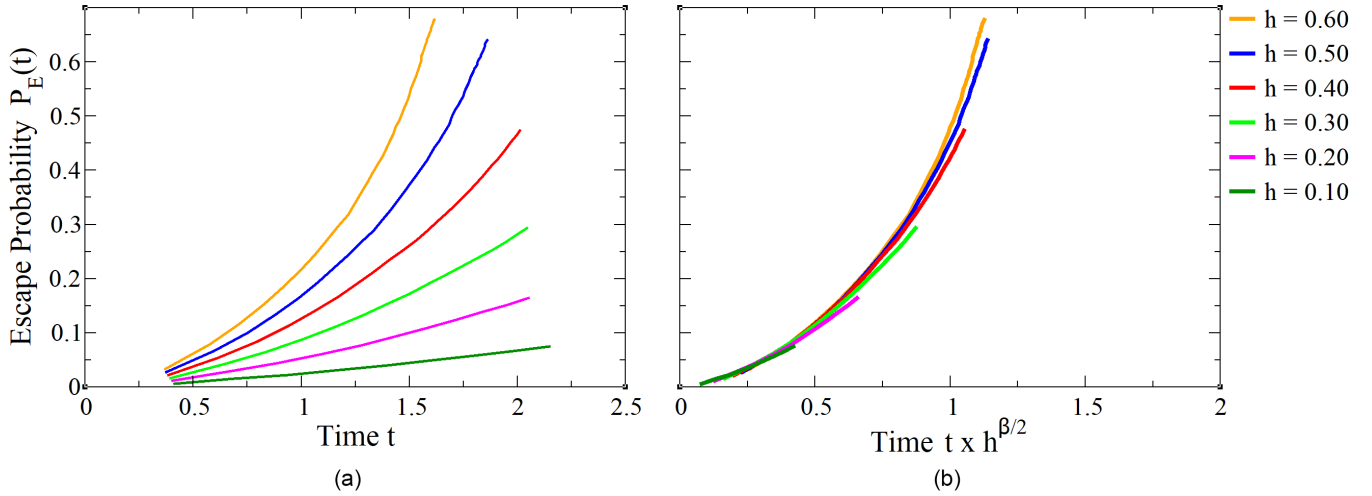


FIG. 3. (a) Plot of the escape probability curves $P_E(t)$ as a function of the time t in seconds, considering hole (pores) sizes in the range $h \in [0.10 \text{ mm}, 0.60 \text{ mm}]$; (b) We show the overlapping of the $P_E(t)$ curves in a single universal curve, indicating the scaling invariance of the escape probability concerning the variations of the hole (pore) size h in the rectangular billiard.

Although the exact size of tomato pollen grains is not detailed in the literature, we consider it reasonable to model pollen as points without interactions, as previous research [14] has demonstrated that predictions of pollen release in tomato flowers are not significantly affected by neglecting pollen grain size.

To keep our approach linked with biological characteristics in a typical buzz pollination process, we considered an ensemble of 3×10^5 noninteracting particles as pollen grains (average amount of pollen grains observed in a *Solanum lycopersicum* flower before any bee visit [32]) inside of the billiard, and we also assumed that all pollen grains are launched from the base of the system, with initial conditions randomly chosen in $x_0 \in (0, a)$ and $\alpha_0 \in (0, \pi)$. Besides, in our approach, we considered initial speeds for each one of the initial conditions of the ensemble equal to the maximum velocity of the wall (in magnitude), denoted by

$$V_0 = |V_{\max_w}| \approx \eta(\omega_1 + \omega_2), \quad (7)$$

where ω_1 and ω_2 represent the angular frequencies of the beat.

To answer our questions, especially concerning scaling invariance, we start by plotting the escape probability $P_E(t)$ as a function of the time t considering different sizes for the apical pore h , through which the particles can escape in the model, as shown in Fig. 3(a). As can be seen, the first result indicates a faster growth for $P_E(t)$ as the size of the hole h increases, which in some way is expected once large pores allow an easy escape of particles in the system. We aim to verify the possibility of scaling invariance for this measure. To explore this, we fitted the data for $P_E(t)$ and observed that it may be approximately described by a power function of the form $P_E(t) = At^2$. Consequently, the scaling hypothesis was evaluated based on the relationship $A \propto h^\beta$, where β represents the critical exponent.

The critical exponent β can be determined through the numerical fitting of A vs. h , as shown in Fig. 4. For the range of holes $h \in [0.10 \text{ mm}, 0.60 \text{ mm}]$ analyzed, the critical exponent is given by $\beta = 1.41(4)$. Once the information about the β exponent is known, we can rescale the horizontal axis

as $\text{Time } t \rightarrow (\text{Time } t) \times h^{\beta/2}$, producing an overlap of the curves presented in Fig. 3(a) to a single and universal plot as shown in Fig. 3(b), indicating the scaling invariance for $P_E(t)$.

Such a result might have important implications for the biological discussion about the buzz pollination process, especially considering that our results indicate that some morphological variabilities observed in nature for the same flower species (as variations on the size of the pore in our model) although might lead to the increasing of pollen release, do not affect the basic mechanisms involved in this process, which might be indicating (for instance) that maximization of the pollen dispersion in some poricidal anthers is much more connected with the pollinating agent characteristics than to the flower itself.

Once our preliminary results indicate that the escape probability is scaling invariant concerning the size of the hole, a natural and complementary question about such a measure is raised: Is the behavior of the escape probability $P_E(t)$ scale invariant due to variations in the billiard geometry?

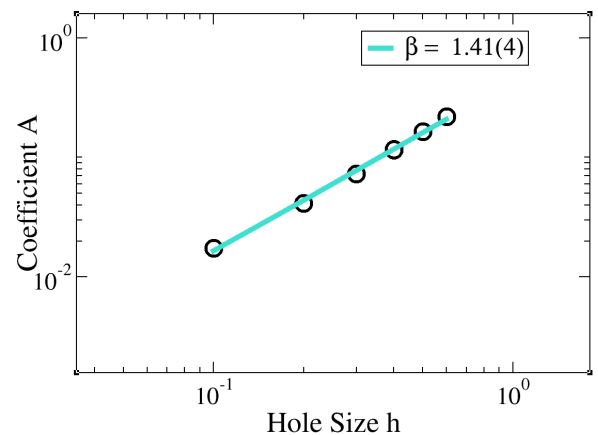


FIG. 4. The behavior of the coefficient A as a function of h (in millimeters) is shown. It follows a power-law relationship, where $A \propto h^\beta$, with an exponent $\beta = 1.41(4)$.

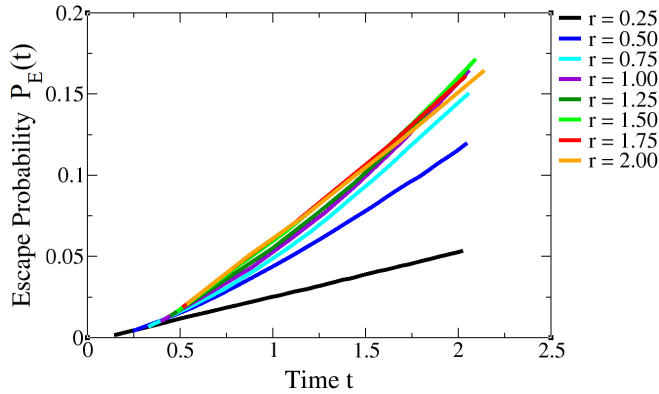


FIG. 5. The plot of the escape probability curves $P_E(t)$ as a function of the time t in seconds, considering different values for the r parameter and $h = 0.20$ mm.

As a simple approach to treat this point, we propose to alter the billiard geometry through the introduction of the parameter r in

$$a_{\text{new}} = ra, \quad b_{\text{new}} = \frac{b}{r}, \quad (8)$$

where essentially r will be responsible for increasing (decrease) the base and the height of the billiard [a, b dimension respectively in Fig. 2(b)], such that the interior area of the system is kept constant for any value of r . Naturally, as we intend to study the implications of the geometry variation, we set $h = 0.20$ mm, which is a value similar to the original pore size.

Under these conditions, we present in Fig. 5 the results considering the escape probability $P_E(t)$ as a function of the time t , but now taking into account different values of the parameter r . As can be observed, $r = 1$ represents the base case, where no variations in the geometry are made [Fig. 2(b)]. On the other hand, when $r = 0.25$, we observe that $P_E(t)$ grows more slowly than for $r \geq 0.5$. In this situation, the height is much larger compared to the base. These variations in the billiard geometry create a scenario where particles spend more time to reach the top of the system, where the hole is. As r increases, the height becomes much smaller than the base, allowing the pollen to reach the top of the anther more quickly and approach the pore position more easily, creating a favorable scenario for the increase of $P_E(t)$ compared to when $r < 1$ (base case). On the other hand, our results indicate that for larger values of r , the escape probability's shape remains almost unchanged, suggesting that this observable is not scale invariant.

IV. DISCUSSION

As a summary, we investigated the dynamics of escaping particles (pollen grains) in a billiard (anther) with boundaries perturbed by vibrations typical of the buzz pollination process in tomato flowers (*Solanum lycopersicum*) caused by bumblebees (*Bombus terrestris*). Our simulations indicate that the escape probability initially exhibits a power law growth. Similar pollen release curves have been observed in natural systems, where the amount of pollen released by

the anthers increases with the duration of vibration (i.e., the number of oscillations) [15]. The escape probability curves are shifted relative to each other, with faster increases associated with larger holes and with some morphological traits, as anther length. Lastly, our results also show that the escape probability presents the property of scaling invariance concerning the hole (pore). These results may have important biological implications, once they suggest that the pore size is the major parameter associated with pollen release.

There are numerous anther architectures among plants bearing buzz-pollinated flowers. Such enormous morphological diversity is related to variation in pore size and geometry. Our study shows that the anther morphology affects pollen release following a simple rule: anthers with smaller pores release pollen grains at a slower rate than those with larger pores. Besides, when $r > 1$, indicating a more horizontal orientation (base is larger than the height) of the anther, the probability of pollen escape does not significantly increase. Conversely, when $r < 1$, indicating a more vertical orientation (the height is larger than base), the pollen release is hindered. Generally, flowers with poricidal anthers offer pollen as the sole reward to buzzing bees, making it a limited resource [33]. Therefore, poricidal anther traits affecting pollen dosing, such as pore size and anther geometry shown here, directly affect plant fitness and probably evolved by natural selection. The pollen release restriction imposed by small pores as well as long anthers may limit the access of pollen for nonbuzzing pollinators distributing the pollen load in several buzzing bees could indeed increase both male and female plant fitness, especially where pollinators are not limited [34]. On the other hand, in places where pollinators are not abundant (e.g., higher altitudes), large pores and short anthers should favor visits of diverse pollinators since pollen release is less restricted. In fact, there are several plant species bearing poricidal anthers pollinated by nonbuzzing insects or even self-pollinated [29,35]. Interestingly, these species feature large pores and short anthers, indicating an adaptive advantage of easy pollen access in such evolutionary scenarios.

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