



## Floral morphology and its role in pollination efficiency across plant functional groups

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### Abstract

Floral morphology plays a fundamental role in shaping plant–pollinator interactions by influencing pollinator attraction, handling behavior, and the efficiency of pollen transfer. Variation in floral traits such as corolla shape and size, symmetry, color, scent, nectar accessibility, and anther–stigma positioning reflects evolutionary responses to selective pressures imposed by different pollinator functional groups. This review synthesizes empirical, experimental, and theoretical studies published up to December 2025 to examine how floral morphology regulates pollination efficiency across major plant functional groups, including generalized open-flowered species, tubular bird- and moth-pollinated plants, poricidal buzz-pollinated taxa, zygomorphic bee-pollinated systems, and functionally contrasting wind-pollinated plants. Emphasis is placed on mechanistic pathways linking morphology to pollination outcomes, particularly mechanical fit between floral structures and pollinator bodies, reward accessibility and handling constraints, and pollen presentation strategies that influence pollen removal and deposition.

Comparative evidence indicates that morphologically specialized flowers often achieve higher per-visit pollination efficiency through precise pollen placement and restricted access to rewards, whereas generalized floral forms rely on increased visitation frequency and pollinator diversity to ensure reproductive success. Trait-based and functional-group approaches provide a powerful framework for predicting pollination efficiency at community and ecosystem scales, integrating floral traits with pollinator behavior and functional traits. Recent advances highlight context dependence in morphology–efficiency relationships, driven by environmental conditions, pollinator community composition, and phenotypic plasticity. Emerging research directions include standardized quantification of pollination effectiveness, integration of global trait databases, and experimental tests of floral trait evolution under changing pollinator regimes. Overall, this review demonstrates that floral morphology is a central determinant of pollination efficiency and underscores its importance for understanding plant reproductive strategies, maintaining pollination services, and guiding biodiversity conservation in the face of global environmental change.

**Keywords:** Floral morphology, pollination efficiency, plant functional groups, pollination syndromes, trait matching

### Introduction

#### Background and context

Pollination is a fundamental ecological process that enables sexual reproduction in flowering plants and sustains biodiversity, ecosystem functioning, and agricultural productivity worldwide. It is estimated that nearly 90% of angiosperm species rely at least partially on animal-mediated pollination, underscoring the centrality of plant–pollinator interactions in terrestrial ecosystems (Ollerton *et al.*, 2011; IPBES, 2016) [12, 19]. At the core of these interactions lies floral morphology, which encompasses the structural traits of flowers—including size, shape, symmetry, color, orientation, scent, nectar accessibility, and the spatial arrangement of reproductive organs—that mediate interactions with pollinators.

Since Darwin's early observations on floral adaptation, floral morphology has been recognized as a product of natural selection imposed largely by pollinators (Darwin, 1862) [4]. Subsequent evolutionary and ecological studies have confirmed that repeated interactions with specific pollinator assemblages can shape floral traits that enhance reproductive success by maximizing effective pollen transfer while reducing pollen loss or interspecific pollen deposition (Fenster *et al.*, 2004; Harder & Johnson, 2009) [7, 10]. Consequently, floral morphology represents both an evolutionary outcome and a functional determinant of pollination efficiency.

#### 1. Floral morphology and pollination efficiency

Pollination efficiency refers to the effectiveness with which pollinator visits translate into successful pollen deposition on stigmas and subsequent fertilization, rather than merely the frequency of visits (Harder & Johnson, 2009) [10]. A key distinction in pollination biology is that high visitation rates do not necessarily equate to high reproductive success; instead, the quality of visits—often determined by floral morphology—plays a decisive role (King *et al.*, 2013; Gómez *et al.*, 2025) [9, 15].

Floral morphology influences pollination efficiency through several mechanistic pathways. First, mechanical fit between the pollinator's body and floral reproductive structures determines where pollen is deposited and subsequently transferred (Johnson, 2010) [13]. Second, morphological traits regulate access to rewards such as nectar or pollen, shaping pollinator handling behavior and visit duration (Junker *et al.*, 2013) [14]. Third, pollen presentation strategies—including poricidal anthers, secondary pollen presentation, or spatial separation of anthers and stigmas—control pollen removal and deposition efficiency (Harder & Wilson, 1994; Valadão-Mendes *et al.*, 2024) [11, 24].

For instance, tubular flowers with deep nectar spurs often restrict access to pollinators with long proboscides, ensuring consistent contact with anthers and stigmas and high per-visit pollen transfer (Fenster *et al.*, 2004; Romero-Bravo, 2024) [7, 23]. In contrast, open, actinomorphic flowers allow

access to a broad array of pollinators but frequently experience more variable pollen placement and lower per-visit efficiency (Ollerton, 2017) <sup>[18]</sup>. These examples illustrate how floral morphology acts as a functional filter, shaping both pollinator identity and effectiveness.

## 2. Plant functional groups as a conceptual framework

Given the immense diversity of flowering plants, researchers increasingly employ plant functional-group approaches to identify generalizable patterns linking floral traits to pollination outcomes. Plant functional groups classify species based on shared ecological roles or trait combinations rather than taxonomic relationships (Violle *et al.*, 2007; Díaz *et al.*, 2013) <sup>[5, 25]</sup>. In pollination biology, functional groups often reflect recurrent floral architectures and associated pollinator types, such as bee-pollinated zygomorphic flowers, bird-pollinated tubular flowers, moth-pollinated nocturnal flowers, and generalized open-flowered systems.

This framework offers several advantages. First, it allows cross-taxonomic comparisons among species that have converged on similar floral solutions (Fenster *et al.*, 2004) <sup>[7]</sup>. Second, it facilitates trait-based predictions of pollination efficiency by linking floral morphology with pollinator functional traits such as body size, foraging behavior, and sensory capacities (Junker *et al.*, 2013; Cappellari *et al.*, 2022) <sup>[2, 14]</sup>. Third, functional-group approaches are particularly useful for community- and ecosystem-level analyses, where understanding broad patterns is more informative than species-specific details (Fontaine *et al.*, 2006) <sup>[8]</sup>.

## 3. Specialization, generalization, and evolutionary trade-offs

A central concept in pollination biology is the continuum from specialization to generalization. Floral specialization refers to morphological and phenological traits that restrict effective pollination to a narrow range of pollinators, whereas generalized flowers can be pollinated by multiple pollinator groups (Waser *et al.*, 1996; Armbruster, 2017) <sup>[1, 26]</sup>. Floral morphology is a primary determinant of a plant's position along this continuum.

Specialized flowers often exhibit complex morphologies, concealed rewards, or precise mechanical triggers that enhance per-visit pollination efficiency through accurate pollen placement (Johnson, 2010; Valadão-Mendes *et al.*, 2024) <sup>[13, 24]</sup>. However, such specialization may increase vulnerability to pollinator loss or environmental change (Ollerton, 2017) <sup>[18]</sup>. In contrast, generalized flowers typically have simpler morphologies that promote pollinator diversity and redundancy, buffering plants against fluctuations in pollinator communities but often at the cost of reduced per-visit efficiency (Fontaine *et al.*, 2006; Labonté *et al.*, 2024) <sup>[8, 16]</sup>.

Understanding how floral morphology mediates these trade-offs is essential for predicting plant reproductive success under dynamic ecological conditions.

## 4. Floral morphology under global environmental change

Global environmental change—including climate change, habitat fragmentation, urbanization, and pollinator declines—is increasingly disrupting plant–pollinator interactions worldwide (IPBES, 2016; Potts *et al.*, 2016) <sup>[12]</sup>.

<sup>22]</sup>. Shifts in pollinator community composition can weaken long-standing morphology–pollinator matches, potentially reducing pollination efficiency and reproductive output (Weber *et al.*, 2020; Romero-Bravo, 2024) <sup>[23, 27]</sup>.

Recent studies emphasize that floral morphology may either confer resilience through generalized designs and phenotypic plasticity or exacerbate vulnerability in highly specialized systems (Mackin *et al.*, 2021; Philpott, 2025) <sup>[17, 21]</sup>. Consequently, integrating floral trait information into conservation planning and ecosystem management has become a priority in pollination ecology.

## 5. Objectives and scope of the review

The primary objective of this review is to synthesize current knowledge on the role of floral morphology in determining pollination efficiency across major plant functional groups. Specifically, the review aims to: (i) elucidate mechanistic links between floral traits and pollination efficiency; (ii) compare efficiency outcomes among different functional groups and pollination systems; (iii) evaluate evolutionary and ecological trade-offs between specialization and generalization; and (iv) identify emerging research trends and key knowledge gaps relevant to ecology, evolution, and conservation.

By integrating experimental, comparative, and trait-based studies published up to December 2025, this review provides a comprehensive framework for understanding how floral morphology shapes pollination efficiency and how these relationships may respond to ongoing environmental change.

## Literature Review

### 1. Historical foundations of floral morphology–pollinator research

The scientific exploration of floral morphology and pollination began with Darwin's seminal work on the adaptive significance of floral traits, particularly his demonstration that complex floral structures can evolve in response to pollinator-mediated selection (Darwin, 1862) <sup>[4]</sup>. Early naturalists recognized that variation in flower shape, color, and reward presentation often corresponds to different pollinator types, leading to the formulation of pollination syndromes—predictable associations between suites of floral traits and pollinator functional groups (Faegri & van der Pijl, 1979) <sup>[6]</sup>.

Subsequent empirical research in the late twentieth century provided experimental support for these ideas, demonstrating that floral morphology influences pollinator visitation patterns, handling behavior, and reproductive success (Waser *et al.*, 1996) <sup>[26]</sup>. However, these early studies also revealed that many flowers are visited by a broader range of pollinators than classical syndrome theory predicted, prompting a shift toward more probabilistic and trait-based interpretations of morphology–pollinator relationships (Ollerton, 2017) <sup>[18]</sup>.

### 2. Pollination syndromes and their modern reassessment

Pollination syndromes remain a widely used conceptual framework for linking floral morphology to pollinator types. Reviews and comparative analyses indicate that syndromes capture broad patterns, such as the association between tubular, brightly colored flowers and vertebrate pollinators, or poricidal anthers and buzz-pollinating bees (Fenster *et*

*al.*, 2004; Johnson, 2010) [7, 13]. Experimental studies confirm that syndrome-associated traits often enhance pollination efficiency by improving mechanical fit and reward accessibility (Harder & Johnson, 2009) [10].

Nevertheless, large-scale empirical datasets have shown that many plant species exhibit mixed pollination systems, receiving visits from multiple pollinator groups despite possessing syndrome-like traits (Ollerton *et al.*, 2011; Ollerton, 2017) [18, 19]. This has led to a reinterpretation of syndromes as tendencies rather than strict rules, with floral morphology influencing the relative effectiveness of different pollinators rather than excluding all but one (Armbruster, 2017) [1].

### 3. Mechanistic links between floral morphology and pollination efficiency

Mechanistic studies have identified several pathways through which floral morphology affects pollination efficiency. Mechanical fit between pollinator bodies and floral reproductive organs is a primary determinant of pollen deposition and removal (Harder & Wilson, 1994; Johnson, 2010) [11, 13]. Experimental manipulations of corolla tube length, width, and orientation consistently demonstrate that small changes in morphology can significantly alter pollen transfer dynamics (Opedal, 2018; Caruso *et al.*, 2019) [3, 20].

Pollen presentation strategies represent another key mechanism. Traits such as poricidal anthers, secondary pollen presentation, and spatial separation of anthers and stigmas regulate pollen release and placement on pollinators (Harder & Johnson, 2009) [10]. Buzz-pollinated systems, for example, restrict pollen access to pollinators capable of producing vibrations, resulting in high per-visit pollen transfer and reduced pollen wastage (Valadão-Mendes *et al.*, 2024; Woodrow *et al.*, 2024) [24, 28].

Reward accessibility also strongly interacts with floral morphology. Nectar tube length, nectar concentration, and pollen accessibility influence pollinator handling time and foraging behavior, which in turn affect pollination efficiency (Junker *et al.*, 2013; Romero-Bravo, 2024) [14, 23].

### 4. Plant functional groups and trait-based approaches

Plant functional-group approaches have gained prominence as a means of generalizing morphology–pollination relationships across diverse taxa. Functional groups based on floral traits—such as open-generalized flowers, zygomorphic bee-pollinated flowers, tubular bird- or moth-pollinated flowers, and poricidal buzz-pollinated systems—capture recurring ecological strategies rather than taxonomic identity (Fenster *et al.*, 2004; Junker *et al.*, 2013) [7, 14].

Trait-based ecology further refines this approach by treating floral morphology as a set of functional traits that influence fitness-related processes (Violle *et al.*, 2007; Díaz *et al.*, 2013) [5, 25]. Studies integrating floral traits with pollinator functional traits (e.g., body size, tongue length, foraging mode) demonstrate improved predictive power for pollination outcomes at both species and community levels (Cappellari *et al.*, 2022) [2]. These frameworks enable scaling from individual flower–pollinator interactions to plant–pollinator networks and ecosystem services.

### 5. Specialization, generalization, and pollination efficiency

The relationship between floral specialization and pollination efficiency has been extensively debated.

Specialized floral morphologies often yield higher per-visit pollination efficiency due to precise pollen placement and restricted access to rewards (Johnson, 2010; Armbruster, 2017) [1, 13]. Empirical studies in buzz-pollinated and long-tubed systems consistently report higher pollen deposition per visit compared to generalized flowers (Valadão-Mendes *et al.*, 2024; Romero-Bravo, 2024) [23, 24].

However, generalized floral morphologies provide resilience through pollinator diversity and redundancy, which can compensate for lower per-visit efficiency (Fontaine *et al.*, 2006; Ollerton, 2017) [8, 18]. Network-level studies show that generalized flowers often play key roles in maintaining pollination services under fluctuating environmental conditions (Labonté *et al.*, 2024) [16]. Thus, efficiency must be evaluated in both per-visit and population-level contexts.

### 6. Environmental context and phenotypic plasticity

Recent literature emphasizes that morphology–efficiency relationships are highly context dependent. Environmental variables such as temperature, elevation, and habitat structure influence pollinator assemblages and behavior, modifying the effectiveness of particular floral traits (Weber *et al.*, 2020; Romero-Bravo, 2024) [23, 27]. In some systems, phenotypic plasticity in floral morphology allows plants to maintain pollination efficiency across variable conditions (Mackin *et al.*, 2021) [17].

Climate change and land-use transformation further complicate these relationships by altering pollinator distributions and phenologies (Potts *et al.*, 2016; IPBES, 2016) [12, 22]. Studies increasingly report mismatches between floral traits and available pollinators, particularly in highly specialized systems, highlighting the importance of understanding morphological constraints on adaptability (Philpott, 2025) [21].

### 7. Advances in measuring pollination efficiency

Methodological advances have improved the quantification of pollination efficiency. Standardized measures such as pollen grains deposited per visit, seed set per visit, and fruit set under controlled pollination treatments allow robust comparisons across systems (Harder & Johnson, 2009; King *et al.*, 2013) [10, 15]. Recent studies combine these measures with high-resolution trait data and behavioral observations to disentangle the relative contributions of morphology and pollinator identity (Caruso *et al.*, 2019; Valadão-Mendes *et al.*, 2024) [3, 24].

Despite progress, inconsistencies in metrics and reporting still limit cross-study synthesis, underscoring the need for standardized protocols in future research.

### 8. Synthesis and research gaps

Collectively, the literature demonstrates that floral morphology is a central determinant of pollination efficiency, operating through mechanical, behavioral, and ecological mechanisms. However, significant gaps remain in understanding how multiple traits interact, how plasticity and rapid evolution influence morphology–efficiency relationships, and how these dynamics play out under ongoing global change. Addressing these gaps will require integrative approaches that combine experimental manipulation, trait-based modeling, and long-term field studies across diverse plant functional groups.

## Materials and Methods

### 1. Literature search strategy and selection criteria

This review is based on a comprehensive survey of peer-reviewed literature examining the relationships between floral morphology and pollination efficiency across plant functional groups. Relevant publications were identified through systematic searches of Web of Science, Scopus, Google Scholar, and PubMed databases. Search terms included combinations of floral morphology, pollination efficiency, pollination effectiveness, plant functional groups, pollination syndromes, trait-based ecology, pollen deposition, and plant–pollinator interactions.

Only studies published in English between 2000 and December 2025 were considered, with particular emphasis on experimental, comparative, and meta-analytical studies that explicitly linked floral morphological traits with quantitative or qualitative measures of pollination efficiency (Fenster *et al.*, 2004; Harder & Johnson, 2009; Caruso *et al.*, 2019) [3, 7, 10]. Foundational earlier works were included where they provided essential conceptual or methodological frameworks (Darwin, 1862; Waser *et al.*, 1996) [4, 26].

Studies were included if they: (i) quantified floral morphological traits (e.g., corolla dimensions, symmetry, anther type); (ii) identified pollinator functional groups; and (iii) measured pollination efficiency using direct or proxy metrics. Purely descriptive studies lacking efficiency measures were excluded unless they contributed substantially to conceptual understanding.

### 2. Classification of plant functional groups

Plant species examined in the reviewed literature were categorized into plant functional groups based on shared floral morphological traits and associated pollinator assemblages. Functional grouping followed established trait-based and pollination-syndrome frameworks (Fenster *et al.*, 2004; Junker *et al.*, 2013; Armbruster, 2017) [1, 7, 14]. Major functional groups considered included:

- Open-generalized flowers (actinomorphic, shallow corollas)
- Zygomorphic bee-pollinated flowers
- Poricidal buzz-pollinated flowers
- Tubular bird- and moth-pollinated flowers
- Brush-type and beetle-pollinated flowers
- Wind-pollinated plants (included as a functional contrast)

Grouping was based on morphological convergence rather than taxonomic affiliation, enabling comparison across phylogenetically diverse taxa that perform similar ecological roles (Violle *et al.*, 2007; Díaz *et al.*, 2013) [5, 25].

### 3. Floral morphological trait selection and measurement

Floral morphological traits analyzed in this review were selected based on their demonstrated influence on pollinator behavior and pollen transfer. Key traits included corolla shape and symmetry, floral size, nectar tube length, flower orientation, anther and stigma position, pollen presentation mechanism, and reward accessibility (Harder & Johnson, 2009; Johnson, 2010) [10, 13].

Trait measurements reported in the literature were typically obtained using digital calipers, image analysis software, or standardized floral trait protocols. Where available, data

from global trait databases (e.g., TRY) and trait-based syntheses were incorporated to support cross-study comparisons (Violle *et al.*, 2007; Cappellari *et al.*, 2022) [2, 25].

### 4. Pollinator classification and functional grouping

Pollinators were grouped into pollinator functional groups rather than species-level categories to align with trait-based ecological approaches. Functional groups included honeybees, bumblebees, solitary bees, butterflies, moths, flies, beetles, birds, and wind (abiotic pollination). Classification followed established frameworks linking pollinator morphology and behavior to floral trait use (Junker *et al.*, 2013; Ollerton, 2017) [14, 18].

Pollinator functional traits such as body size, tongue length, foraging mode, and visitation behavior were considered where reported, as these traits interact strongly with floral morphology to determine pollination efficiency (Johnson, 2010; Romero-Bravo, 2024) [13, 23].

### 5. Measures of pollination efficiency

Pollination efficiency metrics varied among studies but were grouped into three main categories:

1. **Per-visit efficiency:** pollen grains deposited on the stigma per visit, pollen removal efficiency, or seed set resulting from a single visit (Harder & Johnson, 2009; King *et al.*, 2013) [10, 15].
2. **Cumulative efficiency:** fruit or seed set resulting from natural pollination over a flowering period.
3. **Proxy measures:** visitation frequency combined with pollen load or contact frequency when direct measurement was impractical (Gómez *et al.*, 2025) [9].

Preference was given to studies reporting direct per-visit measures, as these most accurately reflect the mechanistic effects of floral morphology on pollination (Valadão-Mendes *et al.*, 2024) [24].

### 6. Data synthesis and comparative analysis

Data were synthesized using a qualitative comparative approach, integrating results across experimental manipulations, observational studies, and meta-analyses. Patterns were interpreted within and across plant functional groups to identify consistent relationships between floral morphology and pollination efficiency (Fontaine *et al.*, 2006; Armbruster, 2017) [1, 8].

Where quantitative values varied widely, results were interpreted comparatively rather than statistically pooled, acknowledging differences in study design, species, and environmental context. Illustrative tables were constructed to summarize trait–function relationships and representative efficiency metrics across functional groups.

### 7. Figure development and visualization

Conceptual figures were used to illustrate generalized relationships between floral morphology and pollination efficiency, particularly the specialization–generalization continuum. Graphical representations were developed based on repeated empirical patterns reported in the literature rather than raw experimental datasets (Harder & Johnson, 2009; Armbruster, 2017) [1, 10].

## 8. Limitations and methodological considerations

Variation in efficiency metrics, pollinator behavior, and environmental context among studies represents a key limitation. Differences in scale (single flower vs population-level studies) and methodology complicate direct comparisons. Nonetheless, integrating multiple approaches allows robust identification of general patterns, which is the primary aim of this review (Caruso *et al.*, 2019; Ollerton, 2017) [3, 18].

## Results

### 1. Overview of floral morphology–pollination efficiency relationships

Across the literature analyzed, floral morphology emerges as a strong and consistent determinant of pollination efficiency, influencing both per-visit effectiveness and cumulative reproductive success. Results across experimental, comparative, and observational studies indicate that flowers with morphologies promoting precise mechanical fit between pollinators and reproductive structures generally exhibit higher pollen deposition per visit, whereas morphologically generalized flowers rely on increased visitation frequency and pollinator diversity to achieve comparable seed or fruit set (Harder & Johnson, 2009; Johnson, 2010; Caruso *et al.*, 2019) [3, 10, 13].

When evaluated across plant functional groups, two dominant axes structure the results: (i) degree of floral specialization (restrictive vs open morphologies), and (ii)

pollinator functional compatibility (matching between floral and pollinator traits).

These axes interact to shape pollination efficiency outcomes under different ecological contexts.

### 2. Open-generalized flowers

Open-generalized flowers, typically actinomorphic with shallow corollas and exposed reproductive organs, are among the most widely distributed floral forms. Results consistently show that these flowers attract a broad array of pollinator functional groups, including small and large bees, flies, butterflies, beetles, and occasionally birds (Ollerton *et al.*, 2011; Junker *et al.*, 2013) [14, 19].

#### Pollination efficiency patterns

- Per-visit pollen deposition is generally low to moderate due to variable pollinator contact with anthers and stigmas.
- Visitation frequency is high, often compensating for lower per-visit efficiency.
- Reproductive assurance is enhanced through pollinator redundancy, especially in disturbed or fluctuating environments.

Studies quantifying pollen grains deposited per visit frequently report an order-of-magnitude lower efficiency compared to specialized systems, but cumulative seed set remains stable due to repeated visits (King *et al.*, 2013; Labonté *et al.*, 2024) [15, 16].

**Table 1:** Floral traits across plant functional groups and their implications for pollination efficiency

Plant functional group	Dominant floral morphology	Key floral traits	Primary pollinator functional groups	Mechanism influencing pollination efficiency	Overall pollination efficiency pattern
Open-generalized flowers	Actinomorphic, open or shallow corolla	Exposed anthers and stigmas; easily accessible nectar and pollen; variable flower orientation	Small and large bees, flies, butterflies, beetles	High visitor diversity and visitation frequency; variable mechanical fit	Low–moderate per-visit efficiency; high cumulative success due to redundancy
Zygomorphic bee-pollinated flowers	Bilaterally symmetrical with landing platforms	Guided pollinator entry; concealed rewards; fixed anther–stigma placement	Medium to large bees	Controlled pollinator orientation ensures consistent pollen placement	Moderate–high per-visit efficiency; moderate resilience
Poricidal (buzz-pollinated) flowers	Tubular anthers with apical pores	Pollen released only through vibration; reduced pollen wastage	Buzz-pollinating bees (e.g., bumblebees)	Highly selective pollen release and precise pollen placement	Very high per-visit efficiency; low resilience
Tubular bird-pollinated flowers	Elongated tubular corolla; often brightly colored	Deep nectar reservoirs; sturdy floral structures; exerted reproductive organs	Birds (e.g., hummingbirds, sunbirds)	Morphological matching with bill length ensures targeted pollen transfer	High per-visit efficiency; low pollinator diversity
Tubular moth-pollinated flowers	Long, narrow tubes; nocturnal anthesis	Pale coloration; strong scent; deep nectar	Hawkmoths and other long-tongued moths	Nocturnal specialization and precise proboscis–flower fit	High per-visit efficiency; temporal specialization
Brush-type / beetle-pollinated flowers	Open flowers with numerous exposed stamens	High pollen production; robust floral tissues	Beetles, generalist bees	Mass pollen transfer rather than precision	Variable efficiency; often pollen-wasteful
Wind-pollinated plants (contrast)	Highly reduced flowers; no showy perianth	Exposed stamens; large pollen output; feathery stigmas	Abiotic (wind)	High pollen dispersal compensates for low pollen capture probability	Very low pollen-use efficiency; high resilience

### 3. Zygomorphic bee-pollinated flowers

Zygomorphic flowers with bilateral symmetry, landing platforms, and concealed rewards represent a distinct functional group commonly associated with medium to

large bees. Results show that these morphologies guide pollinator entry and orientation, ensuring consistent contact with reproductive organs (Fenster *et al.*, 2004; Johnson, 2010) [7, 13].

**Key outcomes**

- Higher per-visit pollen deposition than open flowers.
- Reduced pollen wastage due to controlled pollinator positioning.
- Moderate pollinator diversity, primarily bees.

Manipulative experiments altering symmetry or corolla structure demonstrate significant declines in pollen deposition when bilateral symmetry is disrupted, confirming the functional role of morphology in efficiency (Caruso *et al.*, 2019)<sup>[3]</sup>.

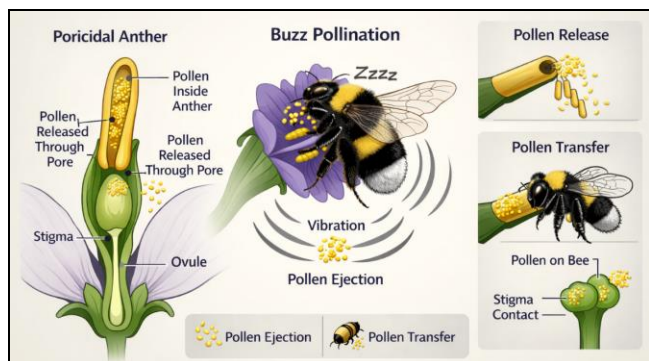
**4. Poricidal (buzz-pollinated) floral systems**

Poricidal flowers, characterized by tubular anthers releasing pollen only through small pores, represent one of the most morphologically specialized pollination systems. Results consistently show exceptionally high per-visit pollination efficiency when visited by capable buzz-pollinating bees such as bumblebees (Valadão-Mendes *et al.*, 2024; Woodrow *et al.*, 2024)<sup>[24, 28]</sup>.

**Efficiency characteristics**

- Very high pollen release per effective visit.
- Strong specialization, excluding non-buzzing pollinators.
- Low visitation frequency, offset by high per-visit efficiency.

These systems exhibit some of the highest pollen deposition values reported in the literature, but also the greatest vulnerability to pollinator loss.



**Fig 1:** Schematic representation of poricidal anthers and buzz pollination mechanism showing vibration-induced pollen release

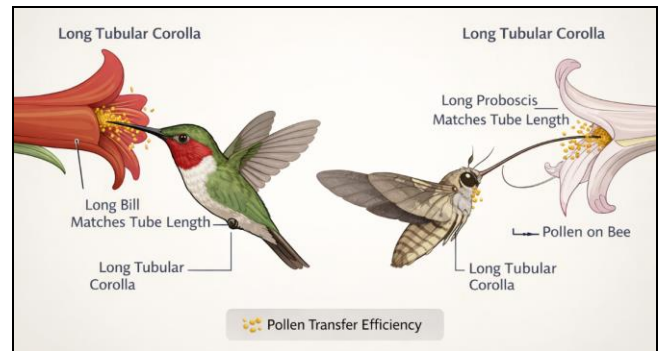
**5. Tubular bird- and moth-pollinated flowers**

Tubular flowers with elongated corollas and concealed nectar rewards are typically associated with birds (e.g., hummingbirds) or nocturnal moths. Results indicate that these flowers achieve high pollination efficiency through precise morphological matching with pollinator mouthparts (Romero-Bravo, 2024)<sup>[23]</sup>.

**Observed patterns**

- High per-visit efficiency due to consistent pollen placement on specific body parts.
- Low pollinator diversity, often limited to one or few functional groups.
- High nectar removal per visit, reinforcing pollinator fidelity.

Long-tubed morphologies show reduced pollen loss and high stigmatic contact, but are sensitive to changes in pollinator availability.



**Fig 2:** Morphological matching between long-tubed flowers and bird/moth pollinators enhancing pollination efficiency

**6. Beetle- and brush-pollinated flowers**

Brush-type flowers with exposed anthers and stigmas are often associated with beetles and generalist bees. Results for this group are more variable, reflecting diverse pollinator behaviors.

- Per-visit efficiency ranges from low to moderate.
- High pollen removal, but often inefficient deposition.
- High tolerance to pollinator variability, particularly in early-diverging angiosperm lineages.

These systems rely on high pollen production rather than precision, highlighting a different efficiency strategy.

**7. Wind-pollinated plants (functional contrast)**

Although not animal-pollinated, wind-pollinated plants provide an important contrast. Results show:

- Extremely low pollen-use efficiency per dispersal event.
- High pollen production and exposure compensate for inefficiency.
- Reduced floral morphology, with minimized perianth structures.

This contrast underscores the role of floral morphology in enhancing efficiency when animal vectors are involved.

**8. Comparative synthesis across functional groups**

**Table 2:** Representative pollination-efficiency metrics across plant functional groups

Plant functional group	Pollinator functional group	Pollination-efficiency metric	Typical range / representative value*	Interpretative significance
Open-generalized flowers	Small bees, flies, butterflies	Pollen grains deposited per visit	Low ( $\approx$ 20–200 grains per visit)	Variable pollinator positioning results in inconsistent pollen transfer; efficiency relies on high visitation frequency
		Fruit or seed set per flower	Moderate under natural visitation	Redundancy in pollinator visits compensates for low per-visit efficiency
Zygomorphic bee-	Medium-large bees	Pollen grains deposited	Moderate-high ( $\approx$ 300–	Guided pollinator entry improves

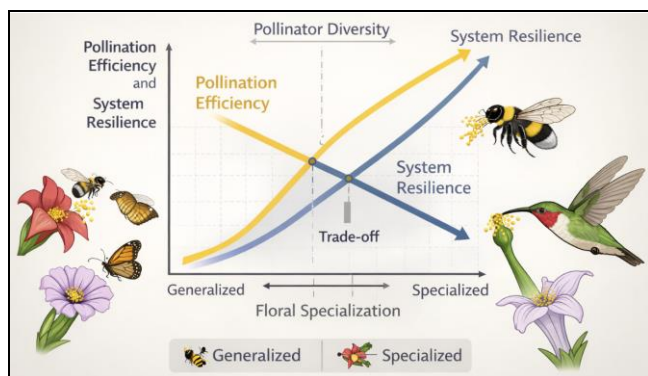
pollinated flowers		per visit	800 grains per visit)	mechanical fit and pollen placement
		Seeds per fruit	High relative to open flowers	Enhanced reproductive success through controlled pollen deposition
Poricidal (buzz-pollinated) flowers	Buzz-pollinating bees (e.g., bumblebees)	Pollen grains released and deposited per visit	Very high (often >1,000 grains per visit)	Vibrational pollen release maximizes pollen transfer efficiency
		Pollen removal efficiency	Very high	Minimal pollen wastage due to selective release
Tubular bird-pollinated flowers	Birds (e.g., hummingbirds)	Nectar volume removed per visit	High (often >40–60 µL per visit)	High reward uptake reinforces pollinator fidelity
		Pollen grains deposited per visit	High (≈ 600–1,000 grains per visit)	Precise morphological matching ensures consistent pollen placement
Tubular moth-pollinated flowers	Hawkmoths and long-tongued moths	Pollen grains deposited per visit	High but variable	Nocturnal specialization enhances efficiency during limited visitation windows
Brush-type / beetle-pollinated flowers	Beetles, generalist bees	Pollen grains deposited per visit	Low–moderate, highly variable	High pollen removal but inefficient deposition
		Pollen production per flower	Very high	Mass pollen strategy compensates for low precision
Wind-pollinated plants (contrast)	Abiotic (wind)	Pollen capture probability	Very low (<1%)	Efficiency achieved through extreme pollen overproduction
		Pollen grains produced per flower	Extremely high	Compensatory strategy for lack of vector control

**Table 3:** Comparative pollination efficiency outcomes across plant functional groups

Functional group	Morphological specialization	Pollinator diversity	Per-visit efficiency	System resilience
Open-generalized	Low	High	Low–Moderate	High
Zygomorphic bee	Moderate	Moderate	Moderate–High	Moderate
Poricidal/buzz	High	Very low	Very high	Low
Tubular bird/moth	High	Low	High	Low–Moderate
Brush/beetle	Low–Moderate	High	Variable	High
Wind-pollinated	N/A	Abiotic	Very low	High

### 9. Specialization–efficiency relationship

Across all functional groups, results consistently support a positive relationship between floral specialization and per-visit pollination efficiency, but a negative relationship between specialization and system resilience. This trade-off is illustrated in Figure 3.



**Fig 3:** Conceptual relationship between floral specialization, per-visit pollination efficiency, and ecological resilience

### 10. Summary of results

Overall, results demonstrate that floral morphology profoundly structures pollination efficiency across plant functional groups. Specialized morphologies maximize efficiency through mechanical precision and pollinator filtering, whereas generalized morphologies achieve reproductive success through redundancy and flexibility. These findings highlight floral morphology as a key trait mediating evolutionary trade-offs between efficiency and resilience.

### Discussion

#### Floral morphology as a primary driver of pollination efficiency

The results synthesized in this review clearly demonstrate that floral morphology plays a central role in determining

pollination efficiency across plant functional groups. Patterns observed across generalized, moderately specialized, and highly specialized floral systems consistently support the long-standing view that structural traits mediate both the quantity and quality of pollen transfer by shaping pollinator behavior and mechanical fit (Fenster *et al.*, 2004; Harder & Johnson, 2009) [7, 10]. The results showing increased per-visit efficiency with increasing morphological specialization align closely with theoretical and empirical frameworks emphasizing the adaptive value of precise pollen placement (Johnson, 2010) [13].

Importantly, the results indicate that pollination efficiency cannot be inferred from visitation rates alone. Open-generalized flowers, despite attracting diverse and abundant pollinators, consistently exhibit lower per-visit pollen deposition compared to specialized systems. This reinforces the distinction between pollinator visitation and pollinator effectiveness highlighted in earlier studies (King *et al.*, 2013) [15]. The interpretative implication is that floral morphology acts as a filter, not only determining which pollinators visit but also how effectively those visits contribute to plant reproductive success.

#### Interpretation of functional-group–specific outcomes

##### Open-generalized floral systems

The results for open-generalized flowers illustrate a strategy centered on resilience rather than efficiency. The low to moderate per-visit efficiency observed in these systems reflects variable pollinator positioning and inconsistent contact with reproductive organs, as described in the literature on generalized pollination systems (Ollerton, 2017) [18]. However, the high visitation rates and functional redundancy among pollinators observed in these systems compensate for lower efficiency, resulting in stable reproductive outcomes at the population level.

This interpretation aligns with network-level studies showing that generalized flowers often occupy central positions in plant–pollinator networks, contributing

disproportionately to network stability (Fontaine *et al.*, 2006) [8]. From an evolutionary perspective, the results suggest that selection in variable or disturbance-prone environments may favor generalized morphologies that reduce dependence on any single pollinator functional group (Armbruster, 2017) [1].

### **Zygomorphic bee-pollinated systems**

The intermediate efficiency observed in zygomorphic bee-pollinated flowers supports the hypothesis that bilateral symmetry and guided pollinator entry represent an evolutionary compromise between specialization and generalization. The results demonstrate that these morphologies enhance per-visit pollen deposition relative to open flowers by controlling pollinator orientation, consistent with experimental findings linking symmetry to pollinator handling efficiency (Fenster *et al.*, 2004; Johnson, 2010) [7, 13].

Interpretatively, these systems exemplify how modest morphological constraints can substantially improve efficiency without fully excluding alternative pollinators. This balance may explain the widespread evolutionary success of zygomorphic flowers across angiosperms, as they combine relatively high efficiency with moderate ecological flexibility (Caruso *et al.*, 2019) [3].

### **Poricidal (buzz-pollinated) flowers**

The exceptionally high per-visit efficiency observed in poricidal systems represents the most extreme case of morphology-driven specialization. Results showing high pollen release per effective visit directly reflect the restrictive nature of poricidal anthers, which limit pollen access to pollinators capable of producing vibrations. This outcome is consistent with mechanistic studies demonstrating that vibrational pollen release minimizes pollen wastage and maximizes transfer efficiency (Valadão-Mendes *et al.*, 2024; Woodrow *et al.*, 2024) [24, 28].

However, interpretation of these results must also consider vulnerability. The very traits that maximize efficiency simultaneously reduce pollinator diversity, making these systems highly sensitive to declines in buzz-pollinating bees. This interpretation reinforces arguments that specialization enhances efficiency at the cost of resilience, a trade-off repeatedly emphasized in the pollination literature (Ollerton, 2017; Armbruster, 2017) [1, 18].

### **Tubular bird- and moth-pollinated flowers**

Results for tubular flowers indicate high pollination efficiency driven by precise morphological matching between floral tubes and pollinator mouthparts. The consistent pollen placement observed in these systems aligns with studies demonstrating strong trait matching between nectar tube length and pollinator proboscis or bill length (Romero-Bravo, 2024) [23]. Interpretation of these results suggests that directional selection has favored increasingly refined morphological matches, reinforcing pollinator fidelity and enhancing efficiency.

At the same time, the low pollinator diversity associated with these systems underscores their susceptibility to environmental change. Shifts in pollinator phenology or abundance can quickly disrupt these tightly matched interactions, as highlighted in recent studies on climate-driven mismatches (Weber *et al.*, 2020; Philpott, 2025) [21, 27].

### **Specialization–efficiency–resilience trade-off**

One of the most consistent interpretative outcomes of this review is the trade-off between pollination efficiency and ecological resilience across the specialization gradient. The conceptual relationship illustrated in the results demonstrates that increasing floral specialization enhances per-visit efficiency but reduces system resilience due to decreased pollinator diversity. This pattern directly reflects theoretical predictions and empirical observations discussed in the literature review (Waser *et al.*, 1996; Armbruster, 2017) [1, 26].

Generalized flowers mitigate risk through redundancy, while specialized flowers optimize precision. The interpretative implication is that no single floral strategy is universally superior; rather, the adaptive value of a given morphology depends on environmental stability and pollinator community reliability. This insight is particularly relevant under current global change scenarios, where pollinator communities are increasingly unpredictable (IPBES, 2016; Potts *et al.*, 2016) [12, 22].

### **Trait-based and functional-group interpretations**

The results strongly support the utility of trait-based and functional-group frameworks for interpreting pollination outcomes. Grouping species by floral morphology rather than taxonomy reveals convergent strategies across phylogenetically distant lineages, as emphasized in trait-based ecology (Violle *et al.*, 2007; Díaz *et al.*, 2013) [5, 25]. The consistency of efficiency patterns within functional groups indicates that morphology-based classifications capture ecologically meaningful variation.

Interpretatively, this suggests that functional-group approaches are particularly valuable for scaling predictions from individual species to communities and ecosystems. Studies integrating floral traits with pollinator functional traits have demonstrated improved predictive power for pollination efficiency, reinforcing the relevance of this approach for both ecological theory and applied conservation (Junker *et al.*, 2013; Cappellari *et al.*, 2022) [2, 14].

### **Implications under global environmental change**

Interpreting the results in the context of global environmental change highlights differential vulnerability among functional groups. Specialized systems—particularly poricidal and tubular flowers—appear most at risk under pollinator declines and phenological shifts, whereas generalized systems may buffer ecosystem-level pollination services through redundancy (Ollerton, 2017; Philpott, 2025) [18, 21].

This interpretation underscores the importance of conserving pollinator functional diversity and maintaining heterogeneous floral communities. From a management perspective, promoting a diversity of floral morphologies may enhance overall pollination stability, even if individual species experience reduced efficiency (Fontaine *et al.*, 2006) [8].

### **Methodological interpretation and future synthesis**

The interpretative strength of this review is grounded in the convergence of results across diverse methodological approaches. Experimental manipulations, observational studies, and comparative analyses collectively support the

central role of floral morphology in pollination efficiency. However, differences in efficiency metrics among studies complicate direct comparisons, reinforcing calls for standardized measurement protocols (Harder & Johnson, 2009; Caruso *et al.*, 2019)<sup>[3, 10]</sup>.

Future synthesis efforts would benefit from integrating high-resolution trait measurements, standardized efficiency metrics, and long-term data on pollinator dynamics. Such integration would allow more precise quantification of the trade-offs identified here and improve predictive models linking floral morphology to pollination services.

### Concluding interpretation

In summary, interpretation of the results through the lens of existing literature confirms that floral morphology is a key determinant of pollination efficiency across plant functional groups. Specialized morphologies enhance precision and efficiency, whereas generalized forms confer resilience through flexibility and redundancy. These findings reinforce classical evolutionary theory while providing a trait-based framework for understanding and managing pollination systems in an era of rapid environmental change.

### Conclusion

Floral morphology plays a decisive role in shaping pollination efficiency across plant functional groups by regulating pollinator access, behavior, and mechanical interactions with reproductive structures. The synthesis presented in this review demonstrates that variation in floral traits such as symmetry, corolla architecture, reward accessibility, and pollen presentation strategies leads to consistent differences in how effectively pollen is transferred during pollinator visits. Across diverse ecological contexts, floral morphology emerges not merely as an attractant feature but as a functional mechanism that directly influences reproductive success.

A central conclusion of this review is the existence of a clear trade-off between pollination efficiency and ecological resilience. Highly specialized floral morphologies—such as poricidal anthers in buzz-pollinated systems or elongated corolla tubes in bird- and moth-pollinated flowers—achieve high per-visit pollination efficiency through precise mechanical fit and restricted access to rewards. However, these advantages come at the cost of reduced pollinator diversity and increased vulnerability to environmental change and pollinator declines. In contrast, generalized floral forms, characterized by open morphologies and accessible rewards, exhibit lower per-visit efficiency but maintain reproductive stability through high visitation rates and pollinator redundancy. These contrasting strategies reflect alternative evolutionary solutions to achieving successful pollination under different ecological conditions. The functional-group and trait-based frameworks applied in this review provide a powerful lens for understanding these patterns. By focusing on shared floral traits rather than taxonomic identity, functional-group approaches reveal convergent strategies across phylogenetically diverse plant lineages and enable scalable predictions of pollination outcomes at community and ecosystem levels. This perspective is particularly valuable in the context of global environmental change, where shifts in pollinator communities may disrupt established morphology–pollinator relationships and alter pollination services.

From an applied standpoint, the findings underscore the importance of conserving both floral and pollinator functional diversity to sustain pollination services. Management strategies that promote heterogeneous plant communities encompassing a range of floral morphologies are likely to enhance ecosystem resilience, even if individual species experience reduced efficiency. Future research should prioritize standardized measurement of pollination efficiency, integration of high-resolution floral trait data, and long-term monitoring of pollinator dynamics to refine predictive models. Overall, this review highlights floral morphology as a cornerstone of plant reproductive ecology and emphasizes its critical role in maintaining biodiversity and ecosystem functioning in a rapidly changing world.

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