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The Evolution and Ecology of Specialized Mutualisms Between Perfume Flowers and Male Euglossine Bees

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Abstract

The unique mutualism between male euglossine bees and the perfume flowers they pollinate in tropical America is one of the most iconic plant–pollinator associations, with a rich body of research incorporating chemical ecology, speciation, and natural history. Male bees collect species-specific blends of compounds from the environment to subsequently use during courtship display. As bees exhibit rapidly evolving olfactory preferences, divergence in floral scent causing visitation by different sets of bee species is thought to drive speciation of the plants via pollinator isolation. Here, we synthesize our current understanding of this specialized system, reviewing the extensive literature on chemical production and diversity in these plants with implications for speciation, and discuss broader patterns from biogeographic and macroevolutionary studies in the group. We highlight gaps in knowledge and propose promising future avenues of research.

1. INTRODUCTION

1.1. Overview of Perfume Flower Biology

From the intricate coevolution between Darwin's orchids and their long-tongued hawkmoth pollinators to the famous bee-like appearance of *Ophrys* orchids and their production of sex pheromones, floral adaptations to animal pollination have long captured the attention of naturalists, scientists, and the general public (Darwin 1862, Raguso 2008). Animal pollination fueled the diversification of angiosperms, driving the evolution of myriad forms of floral signaling to tap into the diverse sensory modalities of their pollinators. These signals, such as color, scent, and humidity, generally advertise the presence of rewards such as nectar or edible pollen to create an integrated floral phenotype (Fenster et al. 2004). However, numerous challenges exist with respect to understanding how signals used by flowers affect the process of pollinator perception and how they relate to rewards. As such, major limitations exist for understanding how signal divergence relates to these evolutionary processes. One unique system in which the signals and rewards are inextricably linked involves the plants pollinated by male euglossine bees.

Euglossine bees, or orchid bees, are some of the most important and iconic insect pollinators in tropical America, providing valuable pollination services to thousands of plant species. This clade of corbiculate bees is united by a unique sex-specific behavior where males acquire odoriferous compounds from environmental sources such as flowers and fungi to concoct perfume mixtures that act as pheromone analogs. Males store these perfumes in specialized hind leg pockets and later expose them during their courtship displays. Female bees, in turn, rely on these chemical signals to obtain critical information on species identity and mate quality (Dressler 1982, Henske et al. 2023, Weber et al. 2016). Perfume signals thus play key roles in mate choice, species recognition, and reproductive isolation in orchid bees.

Perfume making by male orchid bees has given rise to an entire pollination syndrome: androeuglossophily. Androeuglossophilous plants, or perfume flowers, produce floral scents that function as both attractants and their sole rewards, resulting in the evolution of highly specialized plant–pollinator associations (Dodson 1966, Dressler 1968a, Vogel 1963). The syndrome has evolved ~15 times independently across 10 different angiosperm families, most notably in the orchid family, with over 200 species confirmed and likely over 1,000 species estimated to be exclusively pollinated by male orchid bees (**Table 1**) (Ackerman et al. 2023). Perfume flowers offer compelling models to shed light on processes of pollinator-mediated evolution, particularly the study of speciation and adaptation. Scent collection is a sexually selected trait, and olfactory preferences diverge rapidly in the process of euglossine bee speciation (Brand et al. 2020, Henske et al. 2023, Weber et al. 2016). As such, simple changes in floral scent can result in differences in pollinator visitation, driving the process of reproductive isolation. Critically, as the primary attractant is also the reward in perfume flowers, the strategy is distinct from other pollination mechanisms, where the cognitive complexities of signal and reward perception are challenging to untangle.

Almost 60 years after Vogel's (1966) seminal work on the system, plants pollinated by male orchid bees have been the foci of many studies with diverse scopes ranging from chemical ecology to macroevolution. These studies have uncovered many aspects of this pollination system with major implications generally for ecology and evolutionary biology. This review synthesizes our current understanding of male euglossine pollination, from mechanisms of reward production to its distribution across angiosperm lineages. We highlight knowledge gaps and propose avenues of future research to integrate this iconic natural system with modern analytical tools, creating a nexus between sensory biology, speciation, and macroevolutionary research.

Table 1 Taxonomic distribution of exclusively androeuglossophilous species

Group	Number of exclusively androeuglossophilous species	Number of species with pollination data	Number of species in group[a]	Reference(s)
Annonaceae: *Unonopsis*	1	2	48	Teichert et al. 2009, Oliveira et al. 2017
Araceae: *Anthurium*	13	55	1,326	Díaz Jiménez et al. 2019
Araceae: *Spathiphyllum* (Neotropical members)	7	13	49 (Díaz Jiménez et al. 2019)	Díaz Jiménez et al. 2019, 2021
Clusiaceae: *Tovomita*	1	1	77	Nogueira et al. 1998
Euphorbiaceae: *Dalechampia* (Neotropical members)	10–15	90	ca. 100 (Webster & Armbruster 1991, Armbruster 1993)	Armbruster 1993; W.S. Armbruster, personal communication
Gesneriaceae: *Drymonia*	1	2	82	Dressler 1968a
Gesneriaceae: *Gloxinia*	1	1	5	Martel et al. 2019
Orchidaceae: Catasetinae	85	93	354	Ackerman et al. 2023
Orchidaceae: Coeliopsidinae	5	5	19	Ackerman et al. 2023
Orchidaceae: Maxillariinae (*Lycaste*, *Anguloa*, and relatives formerly known as Lycastinae)	6	20	148	Ackerman et al. 2023
Orchidaceae: Oncidiinae (*Trichocentrum*)	1–2	17	106	Ackerman 1983b, Ackerman et al. 2023; J.D. Ackerman, personal communication
Orchidaceae: Oncidiinae twig epiphyte clade consisting of *Macroclinium*, *Notylia*, *Macradenia*, and *Warmingia*	21	21	121	Ackerman et al. 2023
Orchidaceae: Stanhopeinae	115	115	302	Ackerman et al. 2023
Orchidaceae: Zygopetalinae	16	27	418	Ackerman et al. 2023
Solanaceae: *Solanum* section *Cyphomandra*	4	5	50 (Bohs 1991)	Gracie 1993, Sazima et al. 1993, Soares et al. 1989

[a] References are provided for those clades for which data are not available in the Kew database (**https://powo.science.kew.org**).

1.2. A Brief History

Perfume flowers first captured the attention of naturalists in the mid-1800s, most famously being described in Darwin's observations of the charismatic bucket orchids (*Coryanthes*) and *Catasetum* orchids in botanical collections, the latter of which he described as "the most remarkable of all Orchids" (Darwin 1862, p. 211). He detailed how the bizarre morphologies of these flowers likely mediated pollinator movement to facilitate pollen transfer—via a bucket full of liquid with the only escape path requiring contact with the reproductive organs and forceful deposition of pollen packages (pollinaria) triggered by perfume gathering, respectively. These botanical observations provided key evidence for the ability of pollinators to drive the evolution of specialized floral morphologies and attractants. Furthermore, he posited that these orchids were using chemical signaling to attract their pollinators. However, due to a lack of observations with actual pollinators, Darwin was unable to infer more information about the specific complexities of their natural histories, and due to the lack of available technology at the time, characterizing scent profiles was not possible.

The 1960s brought a wave of renewed interest to these plants, with foundational natural history observations conducted by Vogel and Dodson leading to a deeper understanding of the pollinator aspect of perfume flower mutualisms (Dodson 1966, Vogel 1966). Importantly, these authors independently observed that only male bees were visiting flowers and appeared to be gathering scent. These studies paved the way for some of the earliest studies that rigorously characterized floral scent chemistry in any system using gas chromatography coupled with mass spectrometry (GC–MS) (Dodson et al. 1969, Dodson & Hills 1966). The development of these methods represented a pivotal moment in ecological and evolutionary botany, opening novel avenues of investigation into entirely new dimensions of floral trait variation and pollination biology (Fenster et al. 2004, Perkins et al. 2023, Raguso 2008).

Much progress was made in characterizing the interactions between perfume flowers and their pollinators with long-term field studies from the late 1960s to the 1980s, particularly in Panama, Costa Rica, and Ecuador (Ackerman 1983a, Dressler 1968a, Roubik & Ackerman 1987, Williams & Whitten 1983). Many of these studies involved baiting bees with chemical lures and collecting pollinaria attached to their bodies, providing insight into both the compounds that were able to readily attract male bees and the types of orchids that they were likely pollinating. This work provided the foundation for later studies characterizing interaction networks between the plants and their pollinators and identifying the asymmetric nature of these relationships (Ramírez et al. 2011). The discovery of naturalized orchid bees in Florida, where perfume flowers do not occur, further reinforced the notion that while perfume flowers are dependent on bees for pollination, orchid bees are able to obtain their perfumes from other sources (Pemberton & Escalona 2023, Pemberton & Wheeler 2006). Advances in genetic sequencing have led to major breakthroughs in the past decade for the study of perfume flowers. First, genomic studies have been conducted that have characterized the influence of pollinator isolation at the population level. For example, Guizar Amador (2022) performed a rigorous population genetics study coupled with detailed pollination biology, characterizing genetic differentiation and reproductive isolation between sympatric chemotypes of *Gongora* orchids that exhibit similar morphology but distinct scent profiles in southern Costa Rica. Additionally, genomic resources have been developed for *Gongora* cf. *gibba*, allowing for clearer resolution of the mechanistic basis underlying these differences in scent production (Guizar Amador et al. 2024). These studies offer a solid foundation for future research investigating the evolution of perfume flowers at multiple scales of biological organization, from the transcriptomic to the macroevolutionary levels.

2. REWARD PRESENTATION AND DIVERSITY IN PERFUME FLOWERS

2.1. Perfume Flower Reward Presentation

The pattern of high specificity that characterizes the association between male orchid bees and perfume flowers arises from two interacting elements: (*a*) the emission of species-specific volatiles by perfume flowers and (*b*) the species-specific responses that male bees exhibit toward individual compounds and mixtures of compounds. The degree of specificity of these associations varies considerably in the number of bee species involved, from 1 to upward of 10 (N. Rengifo Alfonso, unpublished data; Hernández-Rivera et al. 2024). Understanding scent presentation and production is pivotal for understanding both the structure of mutualistic networks between perfume flowers and bees and the evolutionary dynamics of these interactions. Perfume flowers have evolved from a diverse background of pollination mechanisms as varied as nectar (Gesneriaceae) and resin (Clusiaceae and Euphorbiaceae) rewards, buzz pollination (Solanaceae), and food deception (Orchidaceae). In many groups, floral volatiles are actively emitted from specialized tissues known as osmophores, characterized by a secretory epidermis subtended by a palisade parenchyma rich in starch, the precursor to scent biosynthesis (Vogel 1963).

The positioning of osmophores or other glandular secretory structures varies across radiations of perfume flowers (**Figure 1**). Reward presentation is critical for guiding male bee behavior during visitation and ensures that their bodies are properly aligned with floral reproductive organs during scent acquisition, facilitating successful pollination. For example, in the gesneriad *Gloxinia perennis*, the osmophore is present at the base of the corolla tube typically occupied by the nectary in other species, positioning visiting male bees into contact with the stamens and stigma as they enter the flower to collect perfumes (Martel et al. 2019). In several species of the *Cyphomandra* clade of *Solanum*, osmophores are present on anther connectives, causing expulsion of pollen grains onto the undersides of the bees while they collect perfumes (Sazima et al. 1993). By contrast, osmophores of androeuglossophilous *Dalechampia* species are localized on the stigmatic surfaces (Armbruster et al. 1992). In perhaps the most famous groups of perfume flowers, the orchids of the Cymbidieae tribe, osmophores are present on the surface of the labellum, a modified petal that is often the area of reward presentation across this diverse family (Rudall & Bateman 2002). Perfume collection from these regions allows the flowers to use their famously complex mechanisms to ensure a precise mechanical fit with their reproductive organs.

Another dimension of reward presentation in perfume flowers lies in the timing of scent emission. As with any reward, scent is a potentially costly trait (Vogel 1983), and therefore, pollinator-mediated selection is predicted to generate pressures for maximal production during the times of day when their pollinators are most active. Male orchid bees tend to forage for perfumes in the morning hours, with attenuated behavior later in the day. As such, many perfume flowers exhibit peaks in scent production during these times (Armbruster & McCormick 1990, Martel et al. 2019, Oliveira et al. 2017). Furthermore, a well-documented correlation exists between the timing of foraging in bees and their body size and color, with larger, darker bees tending to forage earlier to avoid overheating (Roubik 1992). As orchid bees vary substantially in these traits, the timing of scent emission may be under strong selection between plants predominately pollinated by bees from different genera (Milet-Pinheiro & Gerlach 2017).

2.2. Chemical Characteristics of Perfume Flower Rewards

While many pollination syndromes are characterized by specific compounds or compound classes, perfume flowers express mostly common floral volatiles, primarily from the monoterpene and phenylpropanoid biosynthetic pathways (**Figure 2*a***) (Gerlach & Schill 1991, Liu et al. 2024). For example, some of the most prevalent compounds present across perfume flowers include monoterpenes such as 1,8-cineole, α-pinene, and myrcene and aromatic compounds such as benzyl acetate and methyl salicylate. All these compounds are present across flowering plants exhibiting a wide variety of pollination systems (Farré-Armengol et al. 2020).

The pool of chemicals used by perfume flowers is far smaller than the very large pool of compounds collected by orchid bees (Ramírez et al. 2011). Additionally, the most abundant compounds found across 65 different species of *Euglossa* were not the same as the most prevalent compounds

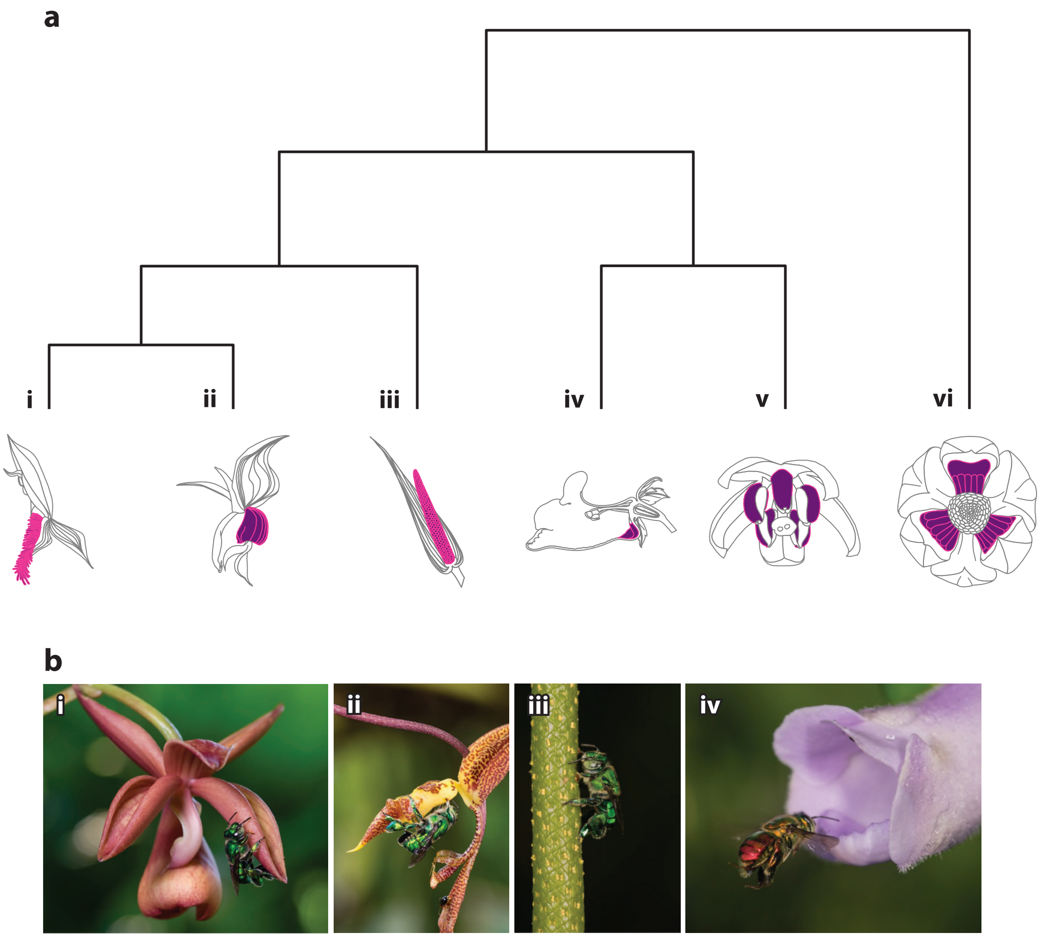

Figure 1

Diversity of reward presentation in perfume flowers. (*a*) The phylogeny shows six independent origins of perfume flowers, while the illustrations show representative taxa along with the location of their scent rewards (*purple*): (*i*) *Catasetum* (Orchidaceae: Catasetinae); (*ii*) *Stanhopea* (Orchidaceae: Stanhopeinae); (*iii*) *Anthurium* (Araceae); (*iv*) *Gloxinia* (Gesneriaceae); (*v*) *Solanum* section *Cyphomandra* (Solanaceae); and (*vi*) *Unonopsis* (Annonaceae). (*b*) The photographs show *Euglossa* bees visiting and collecting scent from (*i*) *Mormodes* sp. (Orchidaceae: Catasetinae), (*ii*) *Gongora* sp. (Orchidaceae: Stanhopeinae), (*iii*) *Anthurium* sp. (Araceae), and (*iv*) *Gloxinia perennis* (Gesneriaceae). Illustrations created by C. P. Gross and photographs copyright T. Eltz.

found in the volatile profiles of 178 species of perfume flowers (**Figure 2*b*,*c***) (Liu et al. 2024, Weber et al. 2016). A key difference between the two datasets was driven by sesquiterpenes (**Figure 2*b*,*c***). Of the most widespread compounds in *Euglossa* hindlegs, 10 of the top 20 were sesquiterpenes, while only one of the 20 most widespread compounds in perfume flower volatiles originated from this pathway. By contrast, monoterpenes make up over half of the most abundant compounds in perfume flowers while comprising only a quarter of the 20 most abundant compounds in hindleg extracts (**Figure 2*b*,*c***). These differences underscore (*a*) the asymmetry of interactions where male bees collect from a large and diverse pool of chemicals including but not limited to perfume flowers and (*b*) the potential chemical constraints of perfume flowers, either due to physiological limits on the production of certain compounds or due to only a limited set of compounds acting as reliable attractants of male euglossine bees.

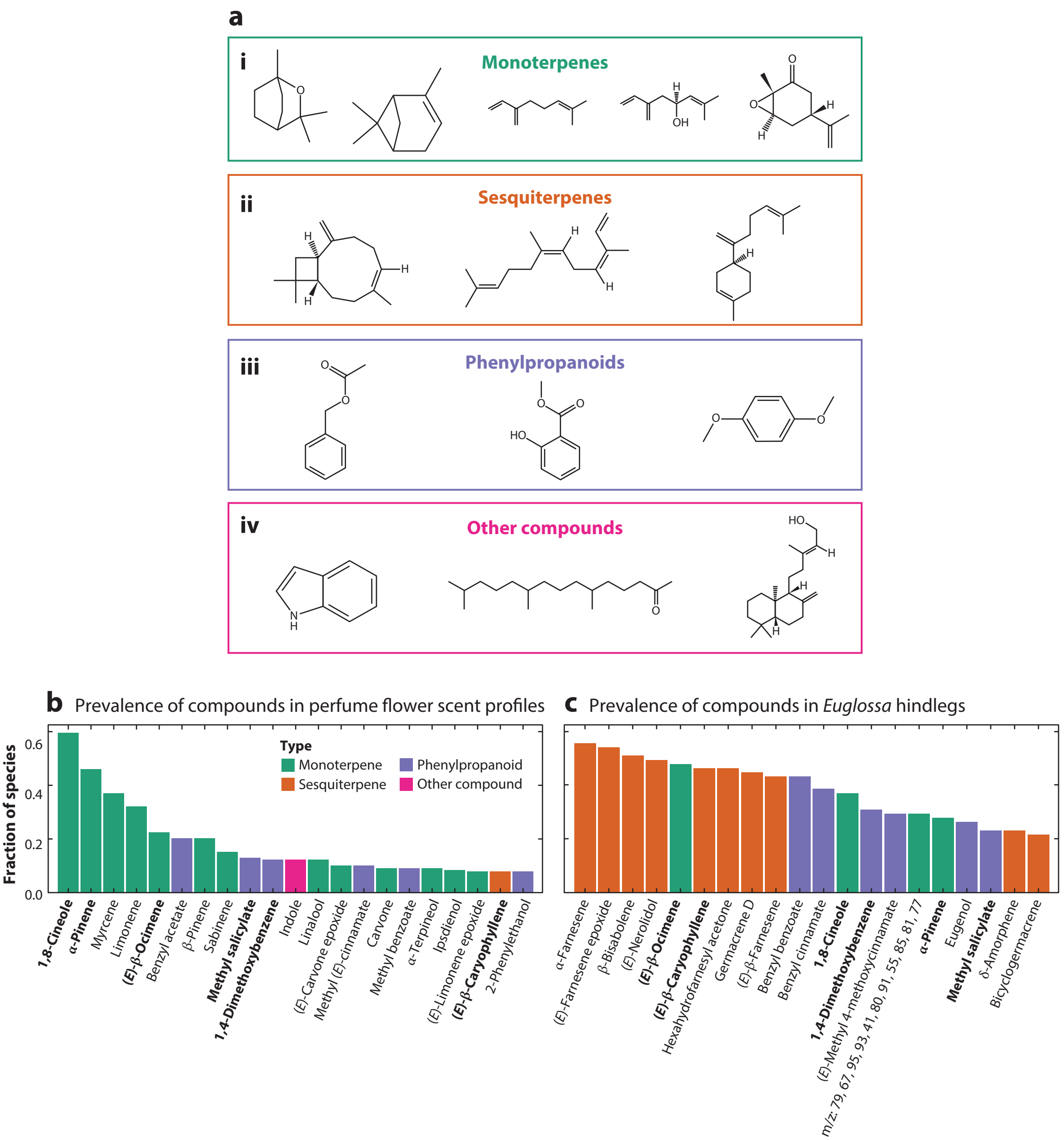

Figure 2

Chemodiversity in perfume flowers. (*a*) Major chemical classes in rewards presented by perfume flowers along with some selected representatives. (*i*) Monoterpenes: 1,8-cineole (general attractant), α-pinene (modifier), β-myrcene (modifier), ipsdienol (private channel for *Euglossa*), and (*E*)-carvone epoxide (private channel for *Eulaema*). (*ii*) Sesquiterpenes: (*E*)-β-caryophyllene, α-farnesene, and β-bisabolene. (*iii*) Phenylpropanoids: benzyl acetate, methyl salicylate, and 1,4-dimethoxybenzene. (*iv*) Other compounds: indole (nitrogenous compound), 6,10,14-trimethylpentadecan-2-one (fatty acid derivative; a semivolatile), and copalol (diterpene; a recently discovered large semivolatile described in Milet-Pinheiro et al. 2021). (*b*) The 21 most widely distributed compounds in perfume flower volatiles, colored by biosynthetic pathway (data from Liu et al. 2024). (*c*) The 20 most widely distributed compounds from *Euglossa* hindleg extracts, colored by biosynthetic pathway (data from Weber et al. 2016). Compounds that are shared between panels *b* and *c* are bolded. Abbreviation: *m*/*z*, mass-to-charge ratio.

Despite the abundance of common floral volatiles, some private chemical channels (Raguso 2008) are used within this pollination system that mediate visitation by specific euglossine bee genera. In particular, the monoterpenes carvone oxide and ipsdienol are highly attractive to male *Eulaema* and *Euglossa* bees, respectively (Milet-Pinheiro & Gerlach 2017). Both compounds are rare in flowers outside of this pollination system and have multiple origins in perfume flowers spanning long evolutionary timescales. As in other pollination systems, there is widespread chemical convergence in perfume flowers, with general patterns across plant orders recapitulated within independent radiations of orchids (Liu et al. 2024).

While nonpolar terpenes and aromatic compounds have been more intensely studied in perfume flowers, several other compound classes have received less attention. For example, skatole, a nitrogenous aromatic compound, is a generalized attractant but to date has not been found in the scent profiles of perfume flowers, despite its presence in several aroid species (Schiestl & Dötterl 2012). The presence of indole, a biosynthetically related compound, in the scent profiles of many aroid perfume flowers suggests that the evolution of skatole and other related compounds could be facilitated by relatively few genetic changes.

Presentation of semivolatiles, heavier compounds with lower vapor pressures, corresponds to an additional mechanism of androeuglossophily, as demonstrated in a bromeliad species that has transitioned away from hummingbird pollination (Milet-Pinheiro et al. 2021). The observation of other male euglossine–pollinated plants with apparent low scent production, such as *Paphinia* orchids (Hentrich et al. 2019), suggests that these compounds could be functioning as further, more cryptic mediators of pollinator attraction and reproductive isolation. To account for these cases, future studies should expand upon methods for scent extraction, using solvent-based methods in addition to the commonly used headspace analyses.

An additional dimension of complexity in floral scent comes from the absolute configurations of the individual compounds present. Several studies have identified stereoselective responses in either attraction of bee species or in triggering antennal responses (Brandt et al. 2019, Schorkopf et al. 2011). For example, the (−)-enantiomer of α-pinene is attractive to males of *Eulaema nigrita*, but neither the (+)-enantiomer or racemic mixtures of both stereoisomers were able to attract bees (Williams & Whitten 1983). Furthermore, the (−)-enantiomer of ipsdienol was found to be attractive to male *Euglossa cyanura* when presented at chemical baits while also triggering neurophysiological responses in excised antennae (Schorkopf et al. 2011).

2.3. Neurophysiological Function of Chemical Rewards and Effects on Ecological Filtering

Recent studies of floral scent have focused on understanding how individual compounds modulate the behavioral and neurophysiological responses of pollinators (Perkins et al. 2023, Raguso 2008). These studies often used electroantennography (EAG), a technique that allows testing of the overall neurophysiological response of an excised antenna to different components within a mixture of compounds (Schneider 1957). These systems offer unique opportunities to disentangle the contributions of individual compounds within mixtures to bee attraction and understand which components of floral scents mediate the attraction of unique bee assemblages and thus cause reproductive isolation through the use of different pollinators.

Individual molecules present in floral scent mixtures can have different effects on bee behavior and thus uniquely contribute to the selective attraction of bee pollinators. A prevailing hypothesis posits that certain compounds act as attractants, drawing in generalized assemblages of bees from long distances, while modifiers act to repel certain bee species, mediating specificity (Gerlach & Schill 1991, Hetherington-Rauth & Ramírez 2016, Williams & Whitten 1983). For example, 1,8-cineole has been identified in all major groups of perfume flowers, is well-known as a generalized bait to attract male bees from different species, and elicited overall moderate to strong responses across bee species tested in an EAG experiment (Brandt et al. 2021, Williams & Dodson 1972, Williams & Whitten 1983). By contrast, α-pinene and myrcene—the other two monoterpenes with the highest prevalence in perfume flowers—generally do not attract diverse groups of bees when presented in pure form and elicited weak EAG responses in the same study. However, experimental studies show that when added to attractive compounds, modifier compounds reduce the attractive potential of the attractive compounds. Whether modifier compounds evolved as adaptations to repel certain pollinators or simply as biochemical by-products of other compounds remains unknown.

To date, there are no known cases of compounds acting synergistically to increase the diversity of attracted pollinators (M.F. Guizar Amador, unpublished data; Williams & Dodson 1972, Williams & Whitten 1983). As such, floral scent complexity is often interpreted as a means of pollinator filtering (**Figure 3*a***). Under this framework, a regional pool of pollinators is initially filtered by specific attractants. Addition of modifier compounds to a mixture containing this

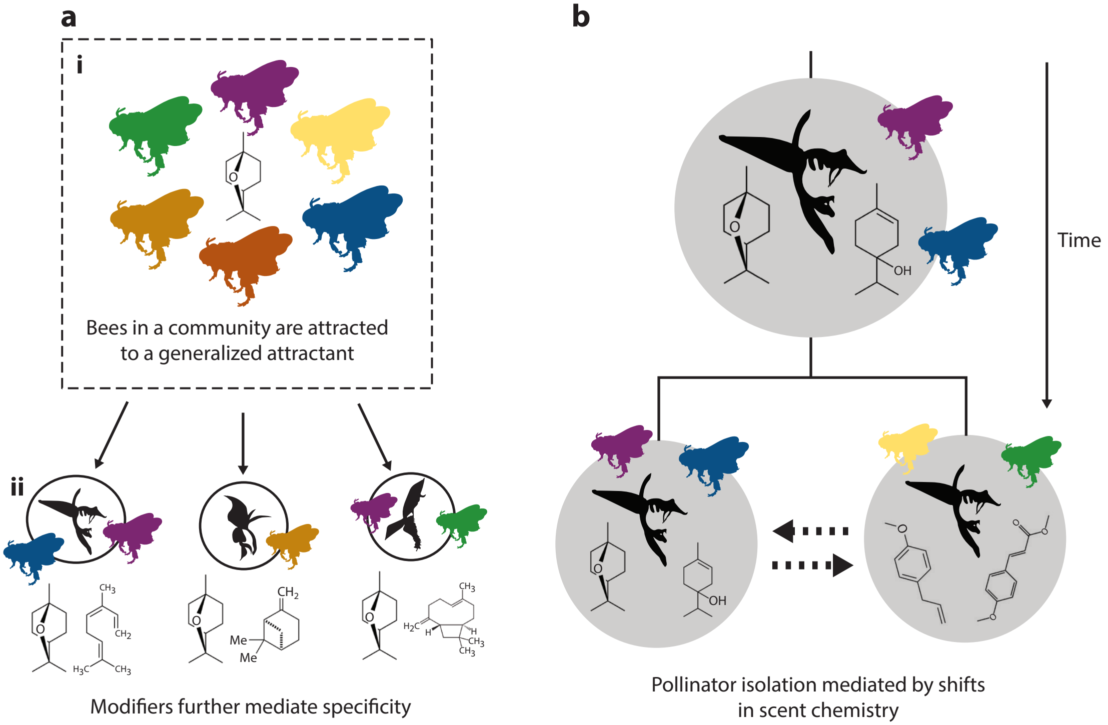

Figure 3

The role of scent in structuring pollinator visitation and isolation in perfume flowers. (*a*) Ecological filtering driven by chemical signaling. (*i*) A regional pollinator community, with different colors corresponding to different bee species, is attracted to a generalized attractant, 1,8-cineole. (*ii*) The different circles show the filtering of this community via modifier compounds (*left to right*, β-ocimene, α-pinene, and β-caryophyllene) in the hypothetical scent profiles of three perfume flower species (shown are a *Gongora*, *Stanhopea*, and *Catasetum*). (*b*) Scent differentiation leading to pollinator isolation. The upper circle shows the scent profile of a hypothetical ancestral *Gongora* population, consisting of the compounds 1,8-cineole and terpinen-4-ol, while the branches correspond to evolutionary shifts in scent production. The right branch shows divergence in scent production within the population toward a scent profile consisting of estragole and methyl methoxycinnamate, resulting in a different set of visiting pollinators and causing reduced gene flow. Bee silhouette created by D.Y. Ramírez.

attractant further filters this pool, resulting in the generation of specificity in this mutualism. In the most extreme cases, plants can restrict their pollinators to single bee species. Truly understanding the adaptive nature of modifiers requires rigorous experimentation using synthetic blends and behavioral trials. Additionally, the relative contributions of attractants and modifiers in mediating the process of reproductive isolation remains an open question.

Comparative EAG studies reveal contrasting patterns at different scales of biological organization. For example, across the orchid bee phylogeny, aromatic compounds produce stronger neurophysiological responses relative to terpenoid compounds (Brandt et al. 2021, Mitko et al. 2016). This pattern could be explained by the presence of olfactory receptor (OR) genes with conserved function. For instance, the OR gene *Or42* in Lepidoptera is known to be narrowly tuned to a single compound—phenylacetaldehyde—that is ubiquitous across flowers (Guo et al. 2021). This receptor is highly conserved across Lepidoptera, and orthologs tested thus far have revealed the same narrow tuning. Future studies should test whether the conserved high sensitivity of male euglossine antennae to aromatic compounds is explained by the higher levels of expression of OR genes that are activated by aromatic compounds relative to those activated by terpenoids. By contrast, EAG responses to certain compounds exhibit phylogenetic signal at the genus level (Brandt et al. 2021). For example, *Euglossa* and *Eulaema* bees exhibited divergent EAG responses to α-copaene, eugenol, ipsdienol, and (−)-(*E*)-carvone. These patterns of sensory bias correspond, at least partially, to the private chemical channels used by perfume flowers that specialize on these bee genera. For example, scent profiles of some perfume flowers pollinated by *Euglossa* have ipsdienol in their floral scent, while flowers pollinated predominantly by *Eulaema* often emit (−)-(*E*)-carvone (Liu et al. 2024, Milet-Pinheiro & Gerlach 2017).

In addition, at the species level, small changes in OR gene sequences can result in vastly different responses to the same compound, creating the impetus for divergence via sexual signaling, such as in the cryptic sister pair *Euglossa dilemma* and *Euglossa viridissima* (Eltz et al. 2008, Brand et al. 2020). A genome-wide analysis revealed that differences in perfume chemistry between the species coincided with rapid divergence in a single locus containing an OR gene (*Or41*). Using functional assays with the empty neuron system—a mutant *Drosophila melanogaster* line that lacks endogenous OR genes—Brand et al. (2020) showed that the derived *Or41* variant present in *E. dilemma* is specific toward its novel major perfume compound (a molecule called HNDB), whereas the ancestral variant of *Or41* present in *E. viridissima* is broadly tuned to multiple odorant compounds, including HNDB, which is absent in the perfume bouquet of *E. viridissima* (Eltz et al. 2008). This example illustrates the rapid evolution of perfume preferences in euglossine bees, an evolving landscape against which perfume flowers have adapted.

Floral scent may also be attractive to florivores, potentially reducing plant fitness. A considerable amount of investigation has gone into this area of study, with compounds having dissuasive function in the scent profiles of several plant species (Kessler et al. 2019). In these cases, suites of floral volatiles that simultaneously attract pollinators and repel florivores may themselves represent a strong filter on the regional pollinator pool. Several studies have noted florivorous weevils attracted to the flowers and buds of androeuglossophilous orchids. These weevils oviposit on the floral tissue and can cause substantial loss of reproductive function (Dressler 1968b, Guizar Amador 2022, Morales-Báez et al. 2016). However, the general degree to which florivory represents a stronger barrier to reproductive success than pollinator limitation across androeuglossophilous species remains to be investigated.

2.4. Perfume Collection in Other Contexts

Perfume flowers in the strict sense use only perfumes for attraction and rewarding of their male euglossine bee pollinators. We note however that there are some cases where perfume collection exists in tandem with other pollination mechanisms. For example, in *Vanilla pompona* male euglossine bees were observed collecting perfumes from the petals and sepals of the flowers (Watteyn et al. 2022). However, pollination occurred only when the same bees entered the tubular labellum in search of nectar rewards that were not provided, demonstrating that food deceit is the actual pollination mechanism. In this case, attraction via perfume on the sterile components of the flowers is either a by-product of scent production or a strategy to increase visitation rates of deceptive flowers with otherwise low levels of attraction.

Opportunistic collection of perfume from scented flowers and other sources is perhaps a common phenomenon, as it has been documented in many systems. For example, male bees have been observed collecting perfumes from sterile tissues of flowers without contacting reproductive organs in *Xiphidium caeruleum* (Haemodoraceae) in Panama (Buchmann 1980) and *Bignonia magnifica* (Bignoniaceae) in Venezuela (Dressler 1968a; referred to in the publication as *Saritaea magnifica*). In the literature, these plants have often been referred to as perfume flowers in subsequent publications, leading to confusion in descriptions of the distribution of androeuglossophily. For precision, we caution against the use of the term perfume flowers for such cases where perfume collection is not associated with pollination. Male bees may also collect perfumes from nonfloral sources, especially when floral sources of perfume components are unavailable (Henske et al. 2025, Pemberton & Wheeler 2006). These observations underscore the asymmetric nature of the perfume flower–orchid bee mutualism, in which plants have repeatedly capitalized on an existing bee behavior. Understanding the evolutionary pathways linking these and other plants with true perfume flowers will provide insight into how this specialized pollination system evolves.

In rare cases, perfume collection by male euglossine bees can also lead to seed dispersal. Recent studies on the seed dispersal of Costa Rican *Vanilla* species have shown that both female stingless bees and male euglossine bees play a role in dispersing the tiny, black seeds of *Vanilla odorata* and *Vanilla planifolia* (Karremans et al. 2023). The orchid bees contribute to the dispersal of these *Vanilla* seeds by actively displacing these while brushing the vanillin-rich inner surface of mature fruits (Karremans et al. 2022). Euglossine bees are expected to contribute to the dispersal of seeds of other fragrant Neotropical *Vanilla* species, but the phenomenon is not known to occur in any other plant.

We note that perfume is also used as a reward for certain *Bulbophyllum* orchids in Southeast Asia (Tan & Nishida 2007). These plants are pollinated by male tephritid flies that use collected compounds as precursors to internally synthesized pheromones. To our knowledge, these are the only examples of perfume rewards outside of the Neotropics. Many members of the genus *Bulbophyllum* use deceptive pollination by dipterans, perhaps mediating the transition to this more complex mechanism. The reasons underlying the paucity of this pollination mechanism in the Paleotropics compared to the myriad origins of perfume flowers in the American tropics could be explained by the greater specificity of the fly pollination system, where only a few specialized compounds are emitted that correspond to a limited number of pheromone precursors. The limited breadth of compounds likely constrains the possibility of evolution toward this chemical niche compared to the ease of transitioning to a perfume flower producing ubiquitous floral volatiles.

3. SPECIATION AND REPRODUCTIVE ISOLATION IN PERFUME FLOWERS

In euglossine bees, perfume collection is critical for species recognition and mate choice. Bee olfactory preferences evolve rapidly, creating a dynamic landscape of sensory biases within a site that plants can exploit in their floral scent profiles. Small changes in floral scent thus have the potential to cause substantial differences in pollinator visitation, driving reproductive isolation between populations of perfume flowers exhibiting subtle differences in scent (**Figure 3*b***).

Historically, this system has been proposed as a potential arena for rapid speciation due to the strong influence of small chemical changes in generating instantaneous prezygotic isolation, and it has often been discussed within the theoretical framework proposed by Grant (1949) and Stebbins (1970) in their foundational work on pollinator-mediated ecological speciation (Dressler 1968a). In this simple model, selection imposed by the preferences of the most effective local pollinators causes floral traits to diverge across populations, leading to the formation of divergent ecotypes early in the speciation process. Several historical studies have provided evidence for this mode of speciation, with the presence of chemotypes of perfume flowers growing in sympatry that appear morphologically similar but exhibit different pollinators (Gregg 1983, Whitten 1985). Recent studies incorporating genetic data have uncovered further evidence, with sympatric chemotypes of *Gongora* orchids in Costa Rica exhibiting population structure concomitant with the differences in their chemical phenotypes and pollinators (Guizar Amador 2022, Hetherington-Rauth & Ramírez 2016).

Understanding the genes underlying floral scent biosynthesis will contribute valuable insights into the proximate mechanisms underlying reproductive isolation in perfume flowers. As many of the compounds in androeuglossophilous scent profiles are ubiquitous floral volatiles with well-studied biosynthetic pathways, candidate gene or pathway approaches can provide insights into these evolutionary processes, mirroring research performed in evolutionary model systems such as *Mimulus* and *Petunia* (Byers et al. 2014, Klahre et al. 2011). Key avenues of research could involve investigating the factors that promote switching between biosynthetic pathways (e.g., terpene to phenylpropanoid) or diversification within a pathway (e.g., monoterpene to sesquiterpene) using gene expression or comparative genomic approaches between incipient species. Additionally, detecting molecular signatures of selection can provide further candidates to help identify loci experiencing the rapid divergence and strong selection that underlie speciation. The recent sequencing and annotation of the *Gongora gibba* genome provides a valuable resource for initiating such studies (Guizar Amador et al. 2024).

The impact of androeuglossophily on speciation dynamics is not well understood across its independent origins. In orchids, particularly in the Stanhopeinae and Catasetinae subtribes, the ease of pollinator transitions has long been thought as a driver of their rapid radiations in a relatively short amount of evolutionary time (200–300 species in ∼20 million years). A macroevolutionary study further identified male euglossine pollination as a driver of more rapid diversification rates in orchids, attributed to the ease with which reproductive isolation can be mediated by simple genetic changes (Givnish et al. 2015). However, this pattern is apparently not universal across the independent origins of the pollination syndrome. For example, the majority of *Dalechampia* are pollinated by female euglossine bees seeking resin for nest building, and the multiple transitions to androeuglossophily in this genus are not associated with dramatic radiations as in the Stanhopeinae and Catasetinae (Armbruster 1993). Furthermore, the prevalence of prezygotic isolation in driving high speciation rates may not be universal due to the emphasis of research on orchids. For example, perfume flowers from the *Cyphomandra* clade of *Solanum* additionally exhibit strong postzygotic barriers to hybridization despite their relatively recent evolutionary history of approximately 6 million years (Bohs 1991, Särkinen et al. 2013).

A tantalizing line of future research involves more detailed study of hybridization in perfume flowers. Hybridization and introgression have become the foci of contemporary speciation research. They have been found to have diverse consequences, from the generation of novel trait combinations that potentially lead to new species formation to the collapse of reproductive barriers between diverged lineages (Edelman & Mallet 2021, Harrison & Larson 2014, Soltis & Soltis 2009). Natural hybrids, while relatively rare, have been identified in perfume flowers, with several studies reporting the existence of hybrid zones (Dodson 1962, 1978). These hybrids offer natural experiments for understanding whether traits important for maintaining species boundaries can be maintained in the face of gene flow. For example, many orchids can be artificially crossed to form fertile hybrids in cultivation. However, the fact that clear hybrids are often rare in natural populations suggests that prezygotic isolation is strong enough to preclude hybridization, selection against hybrids is strong enough that they are unable to reproduce, or some combination of these two mechanisms. Due to the role of chemical signals in perfume flowers as mediators of species boundaries, these are powerful systems for understanding how introgression shapes pre- and postzygotic isolation using a combination of field experiments and population genetic methods.

4. EVOLUTION OF ORCHID BEE POLLINATION IN GEOGRAPHIC SPACE

4.1. Distribution of Euglossine Bees

Euglossine bees are widely distributed throughout the American tropics, ranging from northern Mexico to Argentina. Biogeographic analyses of the Neotropical regions have identified several distinct biogeographic units that harbor endemic taxa of plants and animals (Morrone 2017). While some euglossine bee species exhibit wide ranging distributions throughout the Neotropics (e.g., *Euglossa imperialis*, *Eulaema cingulata*, *Eulaema meriana*, *Eulaema nigrita*, *Exaerete smaragdina*), other species exhibit more restricted distributions that match previously identified biogeographic units. Euglossine bees are primarily found in wet lowlands (<900 m) but have been found in high altitude environments up to 2,640 m in Bolivia (Perger 2015). High-elevation taxa are primarily derived from lowland or generalist ancestors, with few reversals (Ramírez et al. 2010). As with many other montane colonization events in the Neotropics, these transitions were estimated to be recent (<10 Mya), consistent with the recent rapid uplift of the Andes.

Despite an apparent abundance of suitable habitat, orchid bee diversity is depauperate in the Caribbean, with only *Euglossa jamaicensis* found in Jamaica. Interestingly, the only known fossils of orchid bees are two specimens preserved in Dominican amber from 20–30 Mya, suggesting a greater historical range in this area followed by local extinction (Poinar 1998). *E. dilemma*, originally distributed in Central America and Mexico, has recently spread to Florida and the Greater Antilles, likely by accidental anthropogenic means (Pemberton & Escalona 2023). Although perfume flowers are absent in these newly colonized habitats, male bees manage to collect perfume mixtures that are remarkably similar to those collected in the original range (Ramírez et al. 2010), reinforcing the idea that the mutualisms between male orchid bees and perfume flowers encompass an asymmetrical dependence (Ramírez et al. 2011).

The highest species richness of euglossine bees is found in lowland tropical rainforest of both Central and South America. One of the regions with the highest species richness is the northwest Amazon in Ecuador, with as many as 66 species reported for a single site in Napo/Tiputini (Padrón et al. 2018). Other surveyed sites with high species richness of euglossine bee faunas include lowland wet forests of central Panama (44 species) (Roubik et al. 2021) and the Osa Peninsula of Costa Rica (41 species) (T. Eltz, unpublished data). In contrast, sites at the northern and southern edges of the tropical distribution of euglossine bees contain relatively species-poor faunas; for example, the tropical deciduous forests of Chamela, Mexico, harbor nine species (Ayala 2004), and the semideciduous forests of Paraná State in Southern Brazil harbor seven species.

The ancestor of the diverse clade consisting of *Euglossa* + *Eulaema* was estimated to have an Amazonian distribution (Ramírez et al. 2010). *Eufriesea* and several clades within *Euglossa* exhibit a further pattern where branches originating from early nodes lead to lineages present in either Mesoamerica or South America. This pattern suggests a complex history of episodic dispersal events through the proto-Antillean archipelago or the Isthmus of Panama that resulted in apparent disjunct endemism outside of South America (Ramírez et al. 2010).

4.2. Distribution of Perfume Flowers

Mirroring the putative Amazonian origins of many orchid bee lineages, the bulk of perfume flowers are also found in South American lowlands. While many of these plant lineages remain understudied with respect to biogeography, several studies of the diverse Cymbidieae tribe of orchids have sought to elucidate patterns of dispersal and colonization throughout the American tropics (Pérez-Escobar et al. 2017a,b; Tamayo-Cen et al. 2022). The most well-studied group of perfume flowers, the Catasetinae, originated in southeastern South America before spreading to Amazonia approximately 15 Mya, where one lineage evolved androeuglossophily. This lineage underwent greater diversification than its sister lineages, which exhibit rewarding or deceptive pollination and later dispersed to regions of Central America and Mexico (Pérez-Escobar et al. 2017a). Dispersal events were not unidirectional, with some transitions back to South America, as evidenced within the genus *Clowesia* (Tamayo-Cen et al. 2022). Several lineages of the Cymbidieae have additionally extended into montane environments of the Andes and are the highest-growing known representatives of the perfume flowers. For example, *Schlimia alpina* of the Stanhopeinae is reportedly found at elevations of 3,000 m in Colombia and has confirmed visits from perfume-collecting *Eufriesea* sp. in at least part of its range (Van Der Pijl & Dodson 1966; reported as *Schlimia trifida*).

Elevational gradients have been repeatedly demonstrated to generate strong selective pressures on both pollinator communities and floral traits (Galen 1996, Maguiña-Conde et al. 2023). However, to date, no studies have explicitly investigated the role of elevation in structuring interactions between perfume flowers and their pollinators. This is almost certainly due to the lower diversity and overall abundances of bees at these elevations and thus greater difficulty in conducting observations. Higher, colder environments likely present different sensory environments than in the lowland tropics where the bulk of orchid bee research has been carried out, potentially resulting in differences in signal transmission (Koski 2020). Future research could explore how these abiotic factors interact with scent traits and adaptation to pollinators in this specialized system.

An intriguing potential ecological anachronism can be observed in extant orchid communities of the Caribbean. For example, *Dichaea*, *Cochleanthes*, and *Macrodenia* are three genera of orchids that exhibit several cases of male euglossine pollination throughout Central and South America but are also distributed in several Caribbean islands. While rare among mainland species, autogamy has been suggested in five out of the seven *Dichaea* occurring naturally in the Antilles (Ackerman & Collaborators 2014). Notably, populations of the widely distributed *Dichaea hystricina* and *Cochleanthes flabelliformis* in Puerto Rico are reportedly self-pollinating and lack detectable scent (Ackerman 1995, Ackerman & Collaborators 2014). Due to being monoecious, the only *Catasetum* species reported from Cuba is unable to reproduce, with sparse individuals on the island likely originating from wind-dispersed seeds from the mainland (Ackerman & Collaborators 2014). The selfing nature of otherwise outcrossing species suggests a transition to this pollination system following the absence or local extinction of orchid bees. Detailed investigation of these orchid populations, comparing population structure and floral phenotypes with those of continental populations, will provide insight into the trajectories of floral evolution following the removal of pollinators, a particularly important area of study given global climate change.

5. TIMING OF PERFUME FLOWER EVOLUTION

Androeuglossophily is a relatively young phenomenon, with most perfume flower lineages being younger than 20 million years old. Previous phylogenetic studies of perfume flower clades in orchids demonstrated that they were younger than the root of their orchid bee pollinators (∼34 My) (Ramírez et al. 2010), suggesting that orchid perfume flowers evolved by exploiting a preexisting sensory bias rather than via strict coevolution (Ramírez et al. 2011). The most speciose groups of perfume flowers, the Stanhopeinae and Catasetinae orchid clades, exhibit ages of approximately 20 My (Pérez-Escobar et al. 2017a,b, 2024). These ages represent some of the oldest measured for perfume flowers, although lack of comprehensive pollination and species-level phylogenetic studies preclude further comparisons. Notably, these estimates are considerably younger than the oldest clades using other specialized pollination systems such as oil bees (Malpighiaceae at 60 My) (Renner & Schaefer 2010) and hummingbirds (Heliconiaceae at 39 My) (Iles et al. 2017). Perfume flowers have also evolved in the Annonaceae, a member of the magnoliids. Despite the antiquity of the group, this pollination mechanism evolved relatively recently, at least on a similar timescale as the orchids (Massoni et al. 2015).

Most studies of perfume flowers focus on extreme examples that exhibit exclusive androeuglossophily, ignoring cases of mixed pollination. While perfume flowers of the more well-studied Stanhopeinae and Catasetinae (excluding the early diverging and relative species-poor genera *Grobya*, *Cyanaeorchis*, and *Galeandra*) lack other pollinators or even floral visitors besides florivores, this may not be the case across all plants, or even all orchids using this pollination mechanism. We note that there are several groups of plants that exhibit variation with respect to pollination by male euglossine bees. We classify these plants into two groups: (*a*) species with populations that exhibit pollination by both male euglossine bees and other pollinators and (*b*) species that exhibit geographical variation at the population level, with some populations pollinated by male euglossine bees and other populations pollinated by other groups (**Table 2**).

Several examples fall into the former category. For example, a diversity of pollinators consisting of beetles and flies in addition to male orchid bees visit the heavily scented flowers of *Geonoma macrostachys* (Knudsen 2002). Knowledge of the degree to which other pollinators contribute to their reproductive success may allow for a greater understanding into how specialization evolves in incipient perfume flower species. In the Bromeliaceae, *Cryptanthus burle-marxii* exhibits both pollination by hummingbirds, as is characteristic in much of the genus, and pollination by male *E. nigrita* while collecting semivolatiles, potentially reflecting a transition point between the two strategies (Milet-Pinheiro et al. 2021).

To our knowledge, only one case of geographic variation in the use of male orchid bee pollination has been rigorously identified. In the Brazilian *Unonopsis guatterioides*, certain populations exhibit true perfume flowers pollinated by *Eufriesea* males collecting perfumes, while other populations are pollinated primarily by halictid bees seeking pollen (Oliveira et al. 2017). The latter populations are further marked by smaller flower sizes, likely in response to their smaller pollinators, and a different daily schedule of scent emission, with odor plumes released later in the day than the androeuglossophilous populations. The lack of other taxa exhibiting this type of variation is likely due in part to the rarity with which geographic variation in pollination strategies is characterized in the majority of pollination biology studies (van der Niet 2021).

Understanding the evolutionary process of transitioning toward androeuglossophily warrants further investigation. The abundance of opportunistic perfume collection on nonandroeuglossophilous flowers provides evidence that the initial steps of evolving this system through attracting male bees may be readily achievable simply by producing ample amounts of desirable compounds. Sister pair comparisons have been of great utility in understanding the evolution of specialization toward other pollinators such as hummingbirds and oil bees, but such comparisons have not been done in perfume flowers due to the lack of clear cut examples of recent transitions (Castañeda-Zárate et al. 2021, Wessinger 2024). The genera *Drymonia* (Gesneriaceae) and *Trichocentrum* (Orchidaceae) offer promising systems in which to study these transitions. While most species

Table 2 Taxonomic distribution of species with mixed pollination

Clade of origin	Number of species with documented intraspecific variation in androeuglossophily	Other pollinators attracted	Reward sought	Number of species in group[a]	Reference(s)
Annonaceae: *Unonopsis*	1	Small bees (mostly halictids)	Pollen	48	Oliveira et al. 2017
Araceae: *Anthurium*	2	Beetles or small bees	Pollen	1,326	Díaz Jiménez et al. 2019
Araceae: *Spathiphyllum* (Neotropical members)	4	Small bees	Pollen or wax	49 (Díaz Jiménez et al. 2019)	Díaz Jiménez et al. 2019, Díaz Jiménez et al. 2021
Arecaceae: *Geonoma*	1	Dipterans, other bees, and beetles	Pollen at staminate flowers (pollinators may experience deception at pistillate flowers)	68	Knudsen 2002
Bromeliaceae: *Cryptanthus*	2	Hummingbirds	Nectar	63	Filho & Machado 2008, Milet-Pinheiro et al. 2021
Euphorbiaceae: *Dalechampia* (Neotropical members)	1	Female euglossine bees	Resin	90 (Webster & Armbruster 1991)	Armbruster 1993
Pentaphylacaceae (formerly Theaceae): *Ternstroemia* (Neotropical members)	1	*Ptiloglossa*, *Xylocopa*, and *Bombus* bees	Pollen (presumably)	102–105 (Rodriguez-Duque et al. 2021)	Melo 1995
Solanaceae: *Solanum* section *Cyphomandra*	1	Other bees	Pollen	50 (Bohs 1991)	Sazima et al. 1993

[a] References are provided for those clades for which data are not available in the Kew database (**https://powo.science.kew.org**).

in the former genus are thought to be pollinated by both sexes of bees seeking nectar, *Drymonia turrialvae* was observed to be visited only by male bees of a single species of *Eulaema* collecting perfume (Dressler 1968b). Similarly, in *Trichocentrum*, most species are pollinated by bees seeking oil or nectar, but *Trichocentrum capistratum* is androeuglossophilous (Ackerman 1983b, Ackerman et al. 2023). Further chemical and observational studies coupled with well-resolved phylogenies of these genera could produce insight into how opportunistic perfume collection can be coopted by plants to produce more specialized pollination phenotypes.

The degree to which transitions away from androeuglossophily occur is also an open question. In the Stanhopeinae and the Catasetinae, this pollination mode was possessed by their common ancestors and preserved across their respective radiations. However, this pattern is likely not the same across all plants exhibiting this pollination mode, or even across the Cymbidieae orchids. For example, *Warczewiczella lipscombiae* exhibits pollination by orchid bees via food deceit, while several other related genera exhibit perfume flowers (Ackerman 1983b; referred to as *Cochleanthes lipscombiae* in the article). The apparent opportunistic pollination strategy by florivorous weevils in *Dichaea cogniauxiana* may also reflect a transition from androeuglossophily noted in several other members of the genus (Nunes et al. 2018). Both *W. lipscombiae* and *D. cogniauxiana* are members of the Zygopetalinae clade of the Cymbidieae, a highly diverse group of over 400 species that was historically assumed to be primarily pollinated by male orchid bees until recently (Nunes et al. 2017). Further scrutiny of the clade will almost certainly reveal further diversity in strategies and resolve the number of transitions between perfume and non–perfume flowers to provide clarity on the evolutionary lability of this pollination mode.

To date, most pollination biology studies in perfume flowers have been conducted in orchids, biasing our knowledge of their taxonomic distributions. For example, the Gesneriaceae contains approximately 1,200 species in the Neotropics, but only *Gloxinia perennis* and *D. turrialvae* have been confirmed to be perfume flowers, with several other related genera being proposed as candidates. Perhaps the most unexplored frontier of the phylogenetic distribution of perfume flowers lies within Araceae. To date, 13 and 7 species have been confirmed to exhibit exclusive androeuglossophily in the genera *Anthurium* and *Spathiphyllum*, respectively (Díaz Jiménez et al. 2019; *Xanthosoma* is suggested to contain potential perfume flowers in Dodson 1966, but evidence against this interpretation is discussed in Milet-Pinheiro et al. 2017). However, this number is almost certainly a gross underestimate due to the lack of descriptive field studies and the high number of new species awaiting description in the group. Pollination strategies within *Anthurium* are extremely varied and the currently identified species within the genus exhibiting androeuglossophily do not form a clade, suggesting multiple independent origins. The frequency of these origins and the ease in which they transition back to other pollination systems are unknown, in addition to their influences on diversification rates. Further dedicated studies of pollination in a phylogenetic context will provide clarity to these open questions and lead to exciting new fronts of macroevolutionary research complementary to those in orchids.

6. CONSERVATION OF PERFUME FLOWERS AND THEIR INTERACTIONS

Due to the intricacies of their specialized relationships and the imperiled nature of many of their habitats, we would be remiss to not discuss the conservation aspects of perfume flowers. Critically, in asymmetric mutualisms such as those between perfume flowers and euglossine bees, loss of pollinator taxa is predicted to have much stronger negative consequences on androeuglossophilous plant populations than losses in the reverse direction (Ramírez et al. 2011). This may be exacerbated by the fact that many perfume flowers are epiphytic orchids, whose populations are often characterized by low population densities and low rates of pollination (Phillips et al. 2020). Additionally, previous long-term sampling revealed no relationship between degree of specialization in euglossine-pollinated plants and the stability of pollinator populations, suggesting an inherently higher risk of extinction for more highly specialized taxa (Ackerman & Roubik 2012).

As male euglossine bees are relatively easy to sample, multiple studies have characterized the impacts of disturbances such as forest fragmentation and urbanization on their populations. The results of these studies are variable, but most have revealed greater abundance and diversity of orchid bees in nonaltered environments (Aguiar et al. 2015, Allen et al. 2019, Bravo et al. 2022, De Sousa et al. 2022, Hernández-Rivera et al. 2024, Janzen et al. 1982). In contrast, a few have revealed greater abundance and diversity of bees in altered environments (Otero & Sandino 2003) or the absence of differences between these variables (Tonhasca et al. 2002). Therefore, there is a clear tendency for euglossine bee communities to be negatively affected by environmental degradation, although there is variability dependent on environmental characteristics and an effect of the methodologies and attractants implemented (see Brosi 2009).

Despite the myriad studies investigating population trends in euglossine bees, the resulting effects on their dependent populations of perfume flowers have attracted far less attention. In general, Neotropical plants remain underassessed by the International Union for Conservation of Nature (IUCN), and many groups remain data deficient according to this agency. For example, while writing this manuscript only 335 out of the thousands of Neotropical orchid species were evaluated by the IUCN, of which 46 were from genera typically composed of perfume flowers

(IUCN 2024). These challenges make it difficult for impactful policies to be developed to conserve perfume flower populations through changes in land management.

Furthermore, anthropogenic changes have known consequences on the transmission of floral signals such as scent. In particular, ozone and other air pollutants are able to reduce pollinator visitation to flowers by degrading chemical signals used as long-distance attractants (McFrederick et al. 2009, Farré-Armengol et al. 2016), potentially leading to downstream negative effects such as reduced gene flow between populations and lower resilience to further disturbances. How these changes manifest across different forests (e.g., cloud forest versus dry forest) and across different microhabitats within a forest (e.g., the canopy versus understory) remain to be tested and are critical for understanding how androeuglossophilous plants occupying these different sensory environments are affected by anthropogenic stressors. A combined approach using neurophysiological methods and manipulative field experiments will provide much needed insight into how perfume flower populations respond to climate change.

7. CONCLUDING REMARKS

Perfume flowers have long attracted the attention of evolutionary biologists, beginning with Darwin's (1862) observations on the unique pollination mechanisms of *Catasetum*. Rapid acceleration of the field continued with Vogel's (1966) formal characterization of these plants as being pollinated by male bees seeking perfume, followed shortly after by Dodson, Dressler, and colleagues' (1969) foundational use of GC–MS to resolve their chemical profiles. Since then, they have been investigated in great detail in the context of plant–pollinator networks and pollinator-mediated floral evolution. Going forward, incorporating rigorous neurophysiological methods will be of great utility for integrating bee cognition with the complexity of chemical rewards, while multi-omic approaches will allow for greater understanding of how these rewards are produced and evolve across populations and species. These studies should be contextualized within phylogenetic frameworks using the plethora of resources that have become available over the past decade. This research will shed light on the precise mechanisms by which scent differentiation leads to speciation of the perfume flower radiations, some of the most spectacular examples of specialized mutualisms in the world's richest floristic regions. We propose the following series of questions for future research to target that leverage the perfume flower system to understand pollination biology in an eco-evolutionary context.

FUTURE ISSUES

1. How important is multimodal signaling of perfume flowers? Is there an interaction between visual and olfactory cues in short-range signaling? While scent serves as the long-distance attractant and primary reward, the role of visual signaling at short range has not been investigated. Many perfume flowers exhibit finely spotted appearances that may potentially cue into some visual sensory bias expressed by male euglossine bees.
2. Is there geographic variation in rewards and pollinator interactions? How do these mutualisms vary across spatial and temporal scales? Rigorously characterizing the natural history of these plant–pollinator interactions in this manner will provide insight into how population level differences in floral chemistry interact with local bee assemblages, allowing for better insight into how scent differentiation can result in pollinator transitions and the initial stages of reproductive isolation.

3. What are the relative contributions of attractant and modifier compounds to reproductive isolation in perfume flowers? What are the dynamics of chemical evolution in the context of speciation? Understanding this question requires interdisciplinary work integrating the neurophysiology of bees along with the chemical ecology and population genetics of plant populations in the early stages of isolation.
4. What is the role of hybridization in evolutionary processes of androeuglossophilous plants? How do pre- and postzygotic barriers interact to maintain species boundaries? Much of the existing research has focused on prezygotic barriers, but their interactions with other mechanisms remain unexplored. Additionally, the role of adaptive introgression is unknown in these systems.
5. What are the influences of anthropogenic stressors on perfume flower–euglossine bee pollination networks? How will human-mediated changes to the environment affect the future of these mutualisms? As perfume flowers often exist at low densities and rely on scent to attract bees through the dense tangles of tropical forests, pollutants such as ozone have the potential to weaken long-distance olfactory signaling.

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