

Non-floral scent sources of orchid bees: Observations and significance

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Abstract

We observed male euglossines collecting scent at 21 different non-floral sources in Central and South America, strengthening the view that these sources play a central role in euglossine perfume biology. A *Protium* tree provided over 50% of the perfumes for *Eufriesea corusca* and was repeatedly revisited. The co-occurrence of females collecting resin suggests an evolutionary link to male perfume-making.

Abstract in Spanish is available with online material.

KEYWORDS

Costa Rica, Ecuador, Euglossini, French Guiana, orchid bees, perfumes, *Protium*, Suriname

1 | INTRODUCTION

Neotropical orchid bees (Euglossini) are crucial pollinators of many tropical plants, including hundreds of species of orchids (Vogel, 1966; Dressler, 1968; Janzen, 1971). This is facilitated by their distinctive behavior (Dodson & Frymire, 1961), wherein male bees gather exogenous volatiles (Vogel, 1966) and craft individual and species-specific perfume blends (Eltz et al., 1999; Eltz, Roubik, & Lunau, 2005; Zimmermann et al., 2009). These perfumes are exposed during a characteristic display in the forest understory (Eltz, Sager, & Lunau, 2005; Pokorny et al., 2017) and act as intersexual signals to attract females (Henske et al., 2023), arguably reflecting fitness components such as sensory or cognitive acuteness (Henske & Eltz, 2024).

While euglossophilous orchids depend on orchid bees for pollination, studies have shown that this mutualism is one-sided (Ackerman, 1983; Pemberton & Wheeler, 2006), with euglossine-pollinated orchids contributing only a small fraction to the male bees' perfumes (Ramírez et al., 2011). Time-calibrated co-phylogenies suggested that the evolution of euglossophilous orchids occurred comparatively late, at a time when scent-collecting orchid bees had already diversified (Ramírez et al., 2011). Thus, perfume sources other than orchids must have been used at the time the Euglossini originated (Ramírez et al., 2011).

Extant orchid bee males collect volatiles from flowers of various plant families, including Araceae (Ackerman, 1983; Janzen, 1981; Williams & Dressler, 1976), Solanaceae (Sazima et al., 1993; Williams, 1982), Gesneriaceae (Vogel, 1966), Euphorbiaceae

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(Armbruster & Webster, 1979), and Plantaginaceae (Cappellari et al., 2009). However, floral scent sources vary over time, and orchids in particular are scarce due to low population densities and short-lived flowers (Ackerman, 1983).

Orchid bees have been observed performing scent-collecting behavior at non-floral sources such as decaying wood, rotten and ripe fruits, leaf litter, exposed tree roots, bark wounds, decomposed plant tissue, feces, walls sprayed with pesticides, and even from dead conspecifics (Ackerman, 1983; Cappellari & Harter-Marques, 2010; Janzen, 1981; Roberts et al., 1982; Roubik, 1998; Whitten et al., 1989, 1993; Zucchi et al., 1969). Whitten et al. (1993) hypothesized that such sources play a larger role in the concoction of perfumes than previously thought. However, comprehensive reports of non-floral sources are rare and, to our knowledge, the studies by Whitten et al. (1989, 1993) and Eltz et al. (1999) are the only ones that have conducted chemical analyses on such sources. Additionally, it remains unknown how frequently orchid bees visit these sources over time and to what extent these sources contribute to the species-specific perfume.

In this study, we report observations of male orchid bees performing scent-collecting behavior at various non-floral volatile sources at seven localities in Costa Rica, French Guiana, Ecuador, and Suriname (see Appendix S1). We also report female bees collecting resin at non-floral sources.

2 | RESULTS

We encountered 28 (S1–S28) non-floral scent and sap/resin sources attracting either male ($N=20$) or female euglossines ($N=7$), or both ($N=1$; see Table 1, Figure 1, Figure S1). The *Protium* tree (S3), secreting odoriferous sap/resin, was particularly attractive to both male and female euglossines (Figure 1b–d). Here, we observed bees over 2 years and, specifically within a two-month period, made 120 observations of male *Eufriesea corusca* performing scent-collecting behavior. We marked 45 males with numbered plastic tags (see Appendix S1), and 14 of those were resighted on another day (31%; Figure 1c), with six resighted more than once (up to four times). The maximum time span between the first and the last sighting of an individual was 19 days.

For in-depth study of the *Protium* tree, we took resin extracts ($N=3$) from the tree and hind-leg extracts from the male *Ef. corusca* visiting it ($N=13$) to conduct chemical analysis (see Appendix S1). The resin extracts contained mostly sesquiterpenes, with germacrene D, δ -cadinene, α -copaene, an unidentified aromatic compound (molecular weight: 196), and the eudesmane sesquiterpene alcohol junenol as the five most abundant compounds, representing on average 69.3% of the total volatile peak area. Hind-leg extracts from the bees contained 26–48 compounds per individual, with more than half ($53.0\% \pm 6.9$ ($m \pm sd$)) of the compounds also present in the *Protium* resin, accounting for $54.2\% \pm 8.8$ of the total volatile peak area. Three of the five most abundant compounds in the bees' extracts were also found in the resin (junenol: 13.8% peak area,

aromatic compound: 10.0%, germacrene D: 7.9%; see Figure S2). Two major compounds were absent in the resin (methyl cinnamate: 19.0%, unidentified compound; molecular weight: 235, 10.9%; see Figure S2). The relative proportions of the compounds found in both the resin and the bees were strongly correlated (see Figure S3). Some compounds, like the sesquiterpene β -cubebene (see Figures S2 and S4), were present in the resin but not in the bees' perfumes, potentially due to oxidation or reactions with other compounds in the hind legs (Eltz et al., 2019).

3 | DISCUSSION

Our study shows an astonishing diversity and heterogeneity of non-floral scent sources of male orchid bees. Notably, many ($N=16$) sources may involve microbial activity. They were either “decaying”, that is, in a state of microbially assisted decomposition (e.g., S9, S17, S19, S20, S24, S28), or they involved a form of tissue damage that might plausibly result in microbial infection (most other sources). In some cases, the original damage was likely caused by herbivory, such as in S2, a liana where bee activity was restricted to small bark punctures (Figure 1a, Figure S1a). It remains unclear whether the attractive volatiles were emitted by microbes, fungi, or bacteria, or by the plant itself in response to microbial infection (Cappellari & Harter-Marques, 2010; Schoonenberg et al., 2003; Whitten et al., 1989, 1993). The major attractants of S3, a wounded *Protium ravenii*, were likely plant-derived. *Protium* (Burseraceae) resins, commonly known as “copal”, are rich in monoterpenes, sesquiterpenes, and aromatics (Rüdiger et al., 2007).

The *Protium* tree remained attractive to male *Eufriesea corusca* for over two years, eliciting repeated visits. We know of only two other studies that have documented individual euglossine males re-visiting natural fragrance sources (Armbruster, 1993; Janzen, 1981). Other reports of individual re-visitation were either inferential (Armbruster & Webster, 1979) or based on artificial, highly concentrated scent baits (e.g., Ackerman & Montalvo, 1985; Dodson, 1966; Eltz et al., 1999; McCravy et al., 2017; Pokorny et al., 2013, 2015). In contrast to flowers, which are often short-lived and restricted to short flowering seasons, non-floral sources may be more persistent in time and thus more available for orchid bees.

Our findings strengthen the view that non-floral scent sources contribute substantially to male orchid bee perfumes. Previous studies have shown that certain groups of perfume compounds consistently appear together in similar proportions across different individuals and sometimes across species (Eltz et al., 2008; Zimmermann et al., 2009). These recurring combinations of compounds are referred to as “motifs” within the complex blends. It has been assumed that these motifs are building blocks of perfumes collected together from specific sources, albeit the identity of such sources remained obscure. Most motifs are relatively simple, containing three or four structurally related compounds (Eltz et al., 2008; Zimmermann et al., 2009), but larger motifs containing up to eight sesquiterpenes have also been identified (Darragh

TABLE 1 Non-floral scent and resin sources encountered during the course of the study. All observed male bees performed volatile-collecting behavior as described in Dodson & Frymire, 1961.

ID	Month/year	Study site	Source type	Source species (cf.)	Observed bees (#/species/sex)	Remarks
S1	Nov. 2015 Munder	Leaves	<i>Ocimum basilicum</i> (Lamiaceae)	2 <i>El. cingulata</i> ♂♂	obs. only for few consecutive days, despite continued presence of herbs; chewing on leaves with mandibels before collecting	
S2	Mar. 2019 La Gamba	Liana stem (1.5 cm dia)	n/a	<i>El. cingulata</i> ♂♂	Focused on small holes in the bark oozing orange-red sap (1 mm dia; Figure 1a, Figure S1a), >10 obs. of up to 6 ♂♂ for 3w	
S3	Mar. to May 2019–2022 La Gamba	Tree base resin, sap (15 m, dbh 18 cm)	<i>Protium ravenii</i> (Burseraceae)	<i>Ef. corusca</i> ♂♂ <i>Eg. imperialis</i> / <i>asarophora</i> ♀♀	45 ♂♂ marked (Figure 1b,c), 31% re-sighted over 1–19 days, >30 obs. of ♀♀ collecting resin (Figure 1d)	
S4	Mar. 2019 La Gamba	Liana stem	n/a	1 <i>El. cingulata</i> ♀	Exudates on the underside of the stem	
S5	Mar. 2019 La Gamba	Leaf (small tree, height=50 cm)	n/a	1 <i>Eg. imperialis</i> ♂	Dark spot on leaf surface, individual marked, no re-sighting	
S6	Mar. 2019 La Gamba	Tree cut	n/a	1 <i>Ef. cf. corusca</i> ♂	Cutting point of a split and fallen tree Moldy and slightly fruity smell	
S7	Mar. 2019 La Gamba	Branch	n/a	1 <i>El. cingulata</i> ♂	Dark-colored crevice in the bark of a living branch	
S8	Mar. 2019 La Gamba	Tree base	n/a	1 <i>El. cingulata</i> ♂	Moist-looking area on a living tree root close to the soil	
S9	June, Dec. 2019–2021 Cultuurtuin	Sap on stems of dying trees (dbh 80/15/35 cm)	<i>Erythrina poeppigiana</i> (Fabaceae)	<i>El. nigrita</i> ♂♂	Tree wounds, strong smell reminiscent of skatole (Figure S1b), 5 obs. of up to 7 ♂♂	
S10	May to Aug. 2020, 2021 Cultuurtuin	Sap on stems of seedlings/saplings (50 cm, 5 mm dia)	<i>Peltogyne pubescens</i> (Caesalpiniaceae)	<i>El. nigrita</i> ♂♂	Bees were repeatedly biting in the bark, stripped bark sections (Figure 1e); various obs. of multiple individuals	
S11	2020–2023 Munder	Ripe fruit (pods)	<i>Vanilla pompona</i> (Orchidaceae)	<i>El. cingulata</i> ♂♂ <i>Eg. orellana</i> ♂ <i>Eg. sp.</i> ♂	Transfer of seeds and sticky coating to hind-legs (likely inadvertently, Figure 1f); >15 obs. throughout the year 2 obs. of <i>El. cingulata</i> ♂♂ with pollinarium (Figure S1c)	
S12	Mar. 2021 La Gamba	Bark wound (dbh 40 cm)	<i>Tetragastris panamense</i> (Burseraceae)	3 <i>Eg. imperialis</i> ♀♀	Resin collection; stingless bees (<i>Meliponini</i>) also collected at the wound	
S13	Mar. 2021 La Gamba	Wax layer on palm trunk	<i>Socratea exorrhiza</i> (Arecaceae)	1 <i>Eg. cf. gorgonensis</i> ♂	Whitish coating of stem slightly darker at collection spot	
S14	Mar. 2021 La Gamba	Bark wound (dbh 70 cm)	<i>Carapa guianensis</i> (Meliceae)	1 <i>El. cf. polychroma</i> ♀	Resin collection	

(Continues)

TABLE 1 (Continued)

ID	Month/year	Study site	Source type	Source species (cf.)	Observed bees (#/species/sex)	Remarks
S15	Mar. 2021 La Gamba		Feces	<i>Pecari tajacu</i>	1 <i>El. cf. meriana</i> ♀	Loading of feces into corbicula
S16	Mar. 2021 La Gamba		Hinge grease (door)	–	1 <i>Eg. cf. townsendi</i> ♀	Loading of grease into corbicula
S17	Nov. 2021 Route de Kaw		Decaying stems of a liana/lax bush (<5 mm dia)	n/a	>10 <i>Eg. piliventris</i> ♂♂	Stems smelled faintly earthy in places where bees collected (Figure 1g)
S18	Dec. 2021 Montagne des Singes		Roots (0.5–3 mm dia)	n/a	2 <i>El. meriana</i> ♂	Fine horizontal roots eroded from forest floor
S19	Mar. 2022 La Gamba		Leaf margins (dbh 3/3 cm)	<i>Vismia macrophylla</i> (Hypericaceae), <i>Guatteria chiriquensis</i> (Annonaceae)	1 <i>El. cf. polychroma</i> ♂	The two plants were growing adjacent to each other
S20	Nov. 2022 Tiputini		Leaf litter	n/a	1 <i>Eg. sapphirina</i> ♂	Moist, decaying leaves on forest floor
S21	Nov. 2022 Tiputini		Bromeliad leaf	<i>Aechmea</i> sp. (Bromeliaceae)	1 <i>Eg. sp.</i> ♂	Underside of a leaf of a fallen, partly decayed bromeliad
S22	Nov. 2022 Yasuni		Bark wound	<i>Protium</i> sp. (Bursaraceae)	2 <i>El. bombiformis</i> ♀♀ 1 <i>Eg. intersecta</i> ♀ 2 <i>Eg. orellana</i> ♀♀	Resin and sap collection (Figure 1h)
S23	Dec. 2022 Yasuni		Fracture of broken branch	<i>Zanthoxylum</i> sp. (Rutaceae)	1 <i>Eg. intersecta</i> ♂	Sweet fruity smell (Figure S1d), the male focused on innermost layer of thick bark
S24	Dec. 2022 Yasuni		Fruit (2 × 1 cm)	n/a	1 <i>Eg. sp.</i> ♂	Decaying lignified fruit on the forest floor
S25	Nov. 2022 Munder		Ripe fruit (berry)	<i>Triphasia trifolia</i> (Rutaceae)	1 <i>El. nigrita</i> ♂	Sticky sap, strong Citrus fragrance
S26	Jan. 2023 Cultuurtuin		Soil	n/a	3 <i>El. nigrita</i> ♂♂	Bare soil in a ditch with few small roots, no leaf litter, no smell detected
S27	Feb. to Apr. 2023 Munder		Sap of stem of wounded tree	<i>Anacardium occidentale</i> (Anacardiaceae)	1 <i>Ef. surinamensis</i> ♀	3 obs. of collection of exudate, flexible, faint resin smell, <i>Trigona cf. fuscipennis</i> workers also collected at the wound
S28	Mar. 2023 Cultuurtuin		Soil with leaf litter	n/a	2 <i>El. nigrita</i> ♂♂	–

Note: All observed females collected resin or other specified material into their corbiculae.

Abbreviations: dbh, diameter at breast height; dia, diameter; *Ef. Eufriesea*; *Eg. Euglossa*; *El. Eulaema*; obs, observations; w, weeks.

FIGURE 1 (a) *Eulaema cingulata* male performing scent-collecting behavior at liana (S2). (b) *Eufriesea corusca* male performing scent-collecting behavior at *Protium ravenii* (S3). (c) A marked *Eufriesea corusca* male approaching *Protium ravenii* (S3). (d) *Euglossa asarophora* female collecting resin at *Protium ravenii* (S3). (e) *Eulaema nigrita* males biting in the bark of *Peltogyne pubescens* for subsequent volatile collection (S10). (f) Male *Eulaema cingulata* collecting volatiles and seeds from ripe pod of *Vanilla pompona* (S11). (g) *Euglossa piliventris* male performing scent-collecting behavior at liana (S17). (h) *Euglossa imperialis* female collecting resin at *Protium* sp. (S22).



et al., 2023). In our study, the relative proportions of compounds in *Protium ravenii* resin (S3) closely matched those in the perfumes of bees collecting at this source, providing the first unambiguous identification of a source motif in euglossine perfumes. One might argue that *Protium ravenii* represents an obligate scent source for male *Ef. corusca*. However, when we analyzed hind-leg extracts of eight *Ef. corusca* males sampled in central Panama in 2010 (see Appendix S1), we found them to not share the same motif (see Appendix S1). Whether Panamanian *Ef. corusca* did not collect at *Protium ravenii* or whether the composition of its resin differed from that in Costa Rica remains unknown. Additionally, extracts from S23 (bark of *Zanthoxylum* sp.) and a male *Euglossa intersepta* collecting at it (Figure S1d) showed significant overlap in compounds, but their relative proportions were not correlated (see Appendix S1).

It has only recently been established by controlled experiments that the possession of perfume increases male mating

success in orchid bees (Henske et al., 2023). However, it remains unclear what aspect of the perfume, or what specific compound/motif within the blend, is behaviorally relevant. Furthermore, the chemical composition of most non-floral scents produced by the reported sources remains unknown. In some cases, our organoleptic observations allow educated guesses about what the bees were seeking: the wounds of *Erythrina poeppigiana* (S9) smelled of skatole, a pungent nitrogen-containing compound. It attracted male *Eulaema nigrita* (Figure S1b), which are strongly attracted to synthetic skatole baits (Ackerman, 1989). Ripe vanilla pods (S11) smelled of vanillin and attracted *El. cingulata* (Figure 1f) as well as *Euglossa orellana*, both of which are attracted to synthetic vanillin baits in Suriname (B. De Dijn, pers. obs.). Our observations of orchid bee males removing seeds during volatile collection at pods of *Vanilla pompona* align with previous observations on *V. grandiflora* (Lubinsky et al., 2006) and on *V. planifolia* and *V. odorata* (Karremans et al., 2022). Likely, orchid bee males are at the same

time (obligate) pollinators (Figure S1c) and seed-dispersers of various *Vanilla* species.

We also observed female *Euglossa imperialis* and *Eg. asarophora* (Figure 1d) collecting resin from *Protium ravenii*, as well as *Eg. intersecta* and *Eg. orellana* collecting resin from *Protium* sp. in Ecuador (S22, Figure 1h). The use of *Protium* (formerly referred to as *Proteum*) as a resin source for female euglossines has been mentioned in literature (Armbruster, 1984; Dressler, 1982; Rocha-Filho et al., 2012), but these reports were based on tentative observations (Dodson, 1966; “[...] probably collected from *Proteum* spp. [...]”; Zucchi et al., 1969; “[...] probably of resin taken from *Proteum* (Burseraceae)”). However, *Protium* is recognized as a resin source for stingless bees (Barth & Da Luz, 2009; Vit et al., 2024). Although the females and males we observed at S3 did not belong to the same species or even genus, the observations are intriguing and may support the hypothesis raised by Lunau (1992) that “at its outset, the collection of volatiles [...] was linked to the female collection of nest material.” *Protium* resins are rich in terpenoids, some of which are present in euglossine perfumes (e.g., germacrene D, δ -cadinene: Rüdiger et al., 2007; Darragh et al., 2023) and some that are highly attractive when offered in synthetic form (e.g., 1,8-cineole: Dodson et al., 1969; Roubik & Hanson, 2004). Albeit speculative, our observations support the above-mentioned hypothesis by adding the first observation of parallel scent and resin collection in males and females. At the time of the evolutionary origin of male scent collection, resin already played a major role for nest-building female orchid bees (Cameron, 2004). Accidental smell of resin could have conveyed a mating advantage to males due to a pre-existing sensory bias in females, starting the subsequent coevolution of male active scent collection and female scent-based mating preferences (see Arnqvist, 2006).

AUTHOR CONTRIBUTIONS

Conceptualization: TE, JH; Methodology: JH, TE; Investigation: JH, TE, and BDD; Formal analysis: JH; Visualization: JH, TE, BDD; Resources: TE; Funding acquisition: JH, TE; Supervision: TE; Writing – original draft: JH; Writing – review & editing: JH, TE, and BDD.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare ([10.6084/m9.figshare.26179234](https://doi.org/10.6084/m9.figshare.26179234)).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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