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Floral scent chemistry of sympatric species of *Philodendron* (Araceae) sharing a common pollinator in the fragmented coastal Atlantic Forest of southeastern Brazil

Artur Campos Dália Maia ^{a b}  , Stefan Dötterl ^c, Eduardo Gomes Gonçalves ^d,
Ilse Silberbauer-Gottsberger ^e, Gerhard Gottsberger ^e

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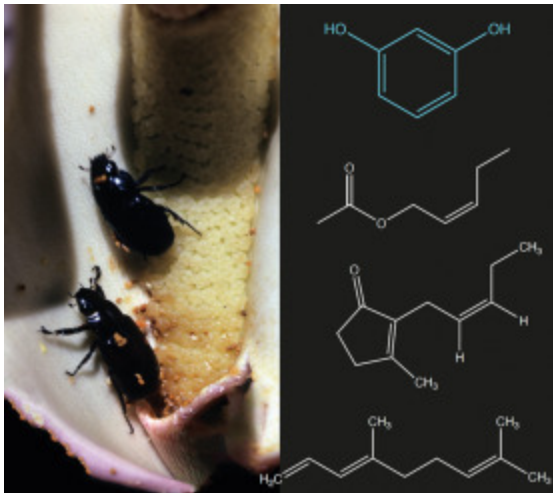
Highlights

- *Cyclocephala variolosa* is the sole pollinator within a rich community of Philodendron;
- Floral fragrances are species-specific with paired similarities among species;
- 47 new VOCs recorded for *Philodendron*. Resorcinol reported for the first time in flowers;
- *Philodendron* spp. pollinated by other cyclocephaline beetles release different scents

Abstract

Floral volatiles are crucial components in flower advertisement, often contributing to the reproductive isolation of angiosperms through scent-mediated differential pollinator attraction. Recently, there were significant advances in our understanding of the chemical communication between plants and cyclocephaline beetles, a predominant group of Neotropical pollinators. However, details on how the floral scent chemistry differs or converges among species pollinated by different or the same cyclocephaline beetle species are still unknown. Here, we used dynamic headspace sampling and gas chromatography coupled with mass spectrometry to investigate the floral fragrance chemistry of eight co-flowering *Philodendron* (Araceae) species that share a single pollinator, *Cyclocephala variolosa* (Melolonthidae, Cyclocephalini). Additionally, we compared our results to published data on the floral fragrances of different conspecifics pollinated by other species of cyclocephaline beetles. Although all the investigated *Philodendron* spp. emitted perceivably intense floral scents, the number of volatile organic compounds in the analyzed samples varied between 1 and 50 among species. Also, the overall relative scent composition strongly differed among species (or chemotypes). The floral scents of four of the investigated species (*P. appendiculatum*, *P. cordatum*, *P. crassinervium*, and *P. eximium*) and one of the two chemotypes of *P. corcovadense* were dominated by (*Z*)-jasnone (46 to 100% total relative concentration). High relative amounts of (*Z*)-2-pentenyl acetate (44 to 66%) characterized the samples of *P. undulatum* and *Philodendron bipinnatifidum*, while (*E*)-4,8-dimethyl-1,3,7-nonatriene was the main constituent in samples of *P. curvilobium* (75%) and the other *P. corcovadense* chemotype (56%). The scents of *Philodendron* spp. pollinated by *C. variolosa* differed from those of conspecifics associated with other cyclocephaline beetle species, but we also verified significant interspecific variation among these species sharing a common pollinator. We hypothesize that this community of co-flowering plants might be reproductively isolated despite being pollinated by the same pollinator species and having partly overlapping scent compositions.

Graphical abstract



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Introduction

The Araceae are a diverse family of monocots with 144 genera and over 3,670 described species (Boyce & Croat 2020), making it one of the five most species-rich monocot families (Christenhusz & Byng 2016). Over 39% of known aroid species are nested within two essentially Neotropical genera, *Anthurium* (~ 950 spp.) and *Philodendron*, which encompasses the subgenera *Philodendron* (~ 460 spp.; Canaletal.2018), *Pteromischum* (~ 80 spp.; Canaletal.2018), and *Meconostigma* (21 spp.; Oliveiraetal.2014). Recently, the subgenus *Meconostigma* has been recognized as the new genus *Thaumatophyllum* Schott by some authors (Sakuraguietal.2018) but not by others (Canaletal.2018; Boyceand Croat 2020).

The vast majority of aroids are entomophilous (i.e., insect-pollinated) and pollinator-driven natural selection is one of the major driving forces behind their diversification (Grayum 1990; Mayoetal.1997; Jímenezetal.2019). Within *Anthurium* and the diverse paleotropical genus *Amorphophallus* (197 spp.; Boyceand Croat 2020), for instance, species radiation/diversification appears to have been associated with both visual (i.e., spathe and spadix colors) and olfactory floral advertisement specialization towards pollination by different groups of anthophilous insects, including fruit flies and gall midges (Diptera), small flower weevils and sap beetles (Coleoptera), oil-collecting bees and orchid bees (Hymenoptera), and thrips (Thysanoptera) (Gibernau2003; Jímenezetal.2019; Claudel2021; Chaiand Wong 2019). Contrastingly, all known species of *Philodendron* share a strict set of morphological and physiological floral traits (see details in Mayoetal.1997) purportedly

evolved in their exclusive association with a unique group of pollinators: cyclocephaline beetles (Melolonthidae, Dynastinae, Cyclocephalini) (Gottsberger and Amaral Jr. 1984; Gibernau et al. 1999).

Pollination in *Philodendron* is crepuscular/nocturnal. During anthesis the inflorescences undergo floral thermogenesis, leading to intense emission of volatile organic compounds (VOCs) that attract the night-foraging cyclocephaline beetles (Gottsberger and Amaral Jr. 1984; Gottsberger and Silberbauer-Gottsberger 1991; Gibernau et al. 1999, 2000; Gibernau and Barabé 2002; Maia et al. 2010; Gottsberger et al. 2013; Pereira et al. 2014; Barbosa et al. 2019; Gibernau et al. 2021). Some authors have also demonstrated the importance of floral thermogenesis in *Philodendron* as an energy reward for the endothermic cyclocephaline beetles (Seymour et al. 2003, 2009), and some species remain thermogenically active throughout the night in what could be interpreted as a strategy to increase beetle activity and efficient pollen transfer (Gottsberger et al. 2013). The inflorescences also function as shelter and rendezvous sites, thus being of central importance to the reproductive ecology of the pollinating beetles (Gottsberger and Silberbauer-Gottsberger 1991; Gibernau et al. 1999).

As observed in other nocturnal pollinators (e.g., moths, bats; Dobson 2006), floral scents are the most important signals used by cyclocephaline beetles to locate receptive *Philodendron* inflorescences under reduced light conditions (Gottsberger and Silberbauer-Gottsberger 1991). Although the general floral morphology is conserved in the genus, the floral scent chemistry is remarkably diverse among the few (i.e., seven) hitherto studied species and can be charted across chemical compound classes of various biosynthetic origins (Knudsen et al. 2006). Moreover, the floral scents of the studied species are dominated (i.e., $\geq 85\%$ of the floral scent composition) either by a single main VOC (*P. adamantinum* Schott and *P. squamiferum* Poepp.) or combinations of two (*P. acutatum* and *P. bipinnatifidum* Schott ex Endl.) to three VOCs (*P. form selloum* C.Koch, *P. mello-barretoanum* Burle-Marx ex G.M. Barroso, and *P. fragrantissimum* (Hook.) G. Don) (Maia et al. 2010, 2019; Gottsberger et al. 2013; Pereira et al. 2014; Gibernau et al. 2021).

The explosive radiation of *Philodendron* is recent (mid-to late-Miocene, ~ 12 mya.; Canalet et al. 2018) and the main diversification centers for the genus largely overlap with those of cyclocephaline scarabs, notably the genus *Cyclocephala* (~ 350 spp.; Moore et al. 2018). Several species of *Philodendron* often occur syntopically in Neotropical forests (Kreft et al. 2004; Croat et al. 2016; Canalet et al. 2019). Due to the lack of functional morphological floral features to filter the access of visitors (Grayum 1990; Mayo et al. 1997), it has been assumed that natural reproductive segregation in *Philodendron* is deeply

associated with the role of floral VOCs in specific pollinator recruitment (Gottsberger et al. 2013; Gibernau et al. 2021). Species can potentially hybridize within the three *Philodendron* subgenera (Mayo 1991; Grayum 1996; Croat 1997), thus, strict pollinator partitioning by distinct floral scent signals could ensure olfactory-mediated pre-zygotic isolation (Smadja and Butlin 2009; Schiestl 2015), reducing interspecific pollen flow that can lead to seed yield depression (Todesco et al. 2016). This idea receives support from the fact that syntopic, co-flowering *Philodendron* conspecifics often utilize different species of cyclocephaline scarabs as effective pollen vectors (Moore and Jameson 2013).

In cases where syntopic populations of different plant taxa attract the same pollinating cyclocephaline beetle species through similar scent bouquets, disjunct flowering periods have been observed (Gottsberger 1989, Maia et al. 2012, 2013). These non-overlapping flowering periods favor intraspecific pollen flow (i.e., reducing pollen mixing) and reproductive isolation, while occasionally promoting pollination facilitation by the temporal partition of pollination services (Feldman et al. 2004; Carreño-Barrera et al. 2020). Referring more specifically to the olfactory preferences of cyclocephaline beetles, certain species exhibit broad chemosensory repertoires and respond to different floral scent attractants (Gottsberger et al. 2013; Maia et al. 2012, 2013, 2019; Pereira et al. 2014). A remarkable example is *Erioscelis emarginata* (Mannerheim, 1829), which for a long time was considered the exclusive pollinator of *P. form selloum* in southeastern Brazil and elsewhere (Gottsberger and Amaral Jr. 1984). During anthesis, inflorescences of *P. form selloum* release large amounts (up to > 6 mg/h) of the methoxylated benzenoids 4-vinylanisole and 3,4-dimethoxystyrene, which attract both male and female *E. emarginata* (Gottsberger et al. 2013). At another location, ~ 800 km to the NNE, individuals of *E. emarginata* were reported as the main pollinators of *P. adamantinum* and were attracted to inflorescences by dihydro- β -ionone, either alone or blended with methyl jasmonate (Pereira et al. 2014). Overall, there have been significant advances in our understanding of the chemical communication between specific plant species and their cyclocephaline beetle pollinators, but it is unclear whether plants that occur in sympatry are reproductively isolated by olfactory means, i.e. by producing different scents that attract different pollinators or by establishing floral constancy within a variety of pollinators. Both of these processes result in high intraspecific pollen flow (Raguso 2008).

The coastal southeastern Atlantic Forest of Brazil is a diversity hotspot for aroids, including *Philodendron*, and is home to no less than 40 species belonging to all three subgenera (Sakuragi et al. 2020). For several years in this area, the two senior authors in the present study (G. Gottsberger and I. Silberbauer-Gottsberger) have investigated a community of eight *Philodendron* species with overlapping flowering periods, seemingly visited (and likely

pollinated) by a single cyclocephaline beetle species. In this study, we conducted a comparative investigation of the floral scent compositions of this species-rich community of *Philodendron*, while also linking our findings to data available from other conspecifics.

Section snippets

Study sites, focal species and historical notes on flowering phenology and pollination ecology

Our main study area is an aroid-diverse region within a coastal Atlantic Forest strip extending for ca. 35 km along the municipalities of Bertioga and São Sebastião (Praia da Boracéia), state of São Paulo (23°51'S, 46°08'W; ~ 8 m.a.s.l.; Fig. 1). Local climate is subtropical and perhumid, with an average annual rainfall of ~ 2,550 mm and air humidity from 80-86% year long. A warm (average 23.2°C) rainy season, from November to March, alternates with a cold (average 19.5°C) dry season, from...

Identity and behavior of flower-visiting cyclocephaline beetles

Cyclocephala variolosa Burmeister, 1847, was the unique beetle species visiting six of the investigated *Philodendron* species at both study sites (Fig. 2d), with the exception of *P. curvilobium* and *P. eximium* for which no beetles were observed to visit inflorescences.

During evening hours, between 17:30h and 02:00h, female and male individuals of *C. variolosa* indiscriminately visited pistillate and staminate inflorescences of different co-flowering species of *Philodendron*. They did not behave as...

Discussion

Our investigation highlighted a unique scenario for highly specialized olfactory-mediated pollination interactions, characterized by the strict dependence of a rich community of conspecific and co-flowering *Philodendron* on a single pollinator species and also on the fact that the floral scent chemistry among these conspecifics is very diverse, roughly constituted of three chemical presentations. Among the identified compounds, 47 were not known to occur in *Philodendron*, and one new floral scent ...

Credit author statement

Artur Campos Dália Maia: Writing- Original draft preparation, Chemical Analyses, Conceptualization. **Stefan Dötterl** Supervision, Data Curation, Writing- Reviewing and Editing. **Eduardo Gomes Gonçalves:** Taxonomy/systematics, Data Validation. **Ilse Silberbauer-Gottsberger & Gerhard Gottsberger:** Methodology, Field work investigation, Data collection....

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper....

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