



Oil flowers for oil bees? pollinator performance confirms partially the pollination syndrome predicted

Suiane S. Oleques^{1,2} · Tatiana T. de Souza-Chies^{1,3} · Rubem S. Avila Jr² 

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Abstract

Oil-producing flowers rely on pollination by oil bees, resulting in a narrow pollination niche. However, some observations have pointed to the high frequency of pollen bee visits widening the spectrum of potential pollinators leading to a more generalist system. In this way, we investigate the role of oil and pollen bees as effective pollinators to better describe the realized pollination niche of these species. We combined visitation frequency data, flowering phenology, pollen deposition on the stigmas and reproductive rates for three oil-producing flowers species in Pampean grasslands from Southern Brazil. *Herbertia pulchella* and *Cypella herbertii* strongly overlapped in their flowering peaks with higher pollination performance of oil bees, while *Kelissa brasiliensis* has its flowering peak temporally separated of them and both bee groups showed similar performances. All of them showed a moderate pollination limitation with fewer values of natural fruit set compared to hand pollinated flowers fruit set. Our results emphasizes the significance of the pollination efficiency difference among pollinator groups contributing to a better understanding of the realized pollination niches of plants. Additionally, we observed that oil bees play a fundamental role for two of the three plant species studied, as predicted by Vogel's pollination syndrome for this particular system with an extremely specialized floral resource. In some conditions, pollen bees may contribute to minimising the variation of fruit set. These findings could aid in understanding the evolution of floral traits in oil flowers of the Iridaceae in a broader context.

Keywords Iridaceae · Pollen bee · Pollinator efficiency · Pollination niche · Reproductive outputs

1 Introduction

The pollination niche is crucial for understanding the processes associated to coexistence of plant species (Johnson 2010; Papuga et al. 2018) and it is determined by floral traits added to pollinator species as well as their attributes and behaviour related to the use of floral rewards. Co-occurring

plant species with similar pollination niche and the temporally available variation in pollinator groups could show differences in the interspecific established interactions leading to the realized pollination niche (Phillips et al. 2020).

Among the floral rewards that determine the structuring of pollination niche, floral oil is used by 360–370 oil-gathering bee species, with some peculiarities compared to other floral rewards, such its nutritional value associated with the food supply of bee larvae, besides the sealing and waterproofing of the brood cell walls of bee nests (Vogel 1974; Buchmann 1987).

Floral oil has evolved several times during angiosperm evolution (Renner and Shaefer 2010; Martins et al. 2015; Possobom and Machado 2017) and the most oil-producing plant groups have subsequently lost this trait in one or more lineages (Renner and Shaefer 2010). Thus, throughout angiosperm evolution, oil secretion as a floral reward has more often been lost than acquired (Renner and Shaefer 2010). Some examples of oil-producing plants are found in plant groups with a prevalence of species with pollen

✉ Rubem S. Avila Jr
rubemavila@gmail.com

¹ Departamento de Botânica, Programa de Pós-Graduação Em Botânica, Universidade Federal do Rio Grande do Sul — UFRGS, Porto Alegre, Rio Grande Do Sul, Brazil

² Laboratório de Pesquisa Em Interações Ecológicas, Universidade Federal Do Pampa - UNIPAMPA, Rua Aloísio Barros Macedo S/N, BR 290 Km 423, São Gabriel, RS 97300-970, Brazil

³ Departamento de Botânica, Universidade Federal Do Rio Grande Do Sul - UFRGS, Av. Bento Gonçalves No. 9500, Porto Alegre, Rio Grande Do Sul 91501-970, Brazil

and nectar reward, as occurs with *Macairea radula* (Bonpl.) DC (Melastomaceae), while some plant groups are typically oil-producing species, such as Malpighiaceae (Vogel 1974). The interactions between oil-producing species and oil bees is found mainly in Neotropics and, despite the low number of studies in many areas of Brazil, the diversity of oil-producing species in well-studied areas (*Caatinga* and *Cerrado*) could reach 9% of the local flora (Carneiro and Machado 2023).

This specific floral reward can be considered an ecological filter that excludes some potential pollinators in favour of specialised oil-collecting bees (Armbruster 2014, 2017), which limits the breadth of the pollination niche (Vogel 1974; Phillips et al. 2020). Nonetheless, plant species with this specialised pollination system could experience some negative consequences, such as high rates of pollen limitation (Wolowski et al. 2014; Lázaro et al. 2015), leading to local extinction in the absence of oil bees (Steiner and Whitehead 1996). This reproductive failure could result from interspecific competition in sympatric plant species with convergence of flowering period. This condition leads to a high proportion of heterospecific pollen deposition on stigmas or loss of visitors (Waser 1983). However, contrasting effects can be observed when the individual fitness is increased by facilitative interaction between the sympatric plants sharing the pollinators (Ratchke 1983). In this way, plant species with some flexibility in terms of dependence on oil bee could be associated with a broad pollination niche, and their fruit and seed-set could be enhanced by other pollinator functional groups, mainly exclusively pollen-collecting bees (Steiner and Whitehead 1996; Manning and Goldblatt 2002; Pauw and Bond 2011; Oleques et al. 2020) decreasing the potential negative effects of interspecific competition by pollinators. Indeed, several oil bee-pollinated plant species have reduced or eliminated their dependence on oil-collecting bees locally or, in the long term, through the loss of oil-secreting structures (Cocucci 1991; Steiner and Whitehead 1996; Chauveau et al. 2012). Despite their pollination service, pollinators that are not specialised in oil collection (pollen bees) could act on the evolutionary history of this particular plant guild (Oleques et al. 2020), reconfiguring the pollination niche in these plants. In this way, the observed shifts in the secretory structure and reward offered could result from these pollination niche changes (Steiner 1993, 1998; Steiner and Whitehead 1996; Goldblatt and Manning 2006).

Pollinators of different species or functional groups often differ in their performance and effectiveness in pollination and vary in the number of pollen grains removed or deposited. Therefore, the pollinator performance can be related to strength of selection pressure on floral traits (Stebbins 1970; Harder and Johnson 2009) as the oil secreting structures. However, direct estimates of pollinator performance added to the visitation frequency of different pollinators are scarce

(Koski et al. 2018). Oleques et al. (2020) concluded from visitor frequency and pollen exported a possible ecological differentiation of pollination niches between some Iridaceae species. However, pollen exported on the pollinator's body does not necessarily imply correct deposition on the stigmas of conspecific individuals. Pollen losses during flight or the use by bees on the larval diet could significantly reduce the amount of pollen reaching the stigmas. In addition, visitation frequency may not mean a realistic indicator of pollinator efficiency (King et al. 2013). Added to this, the quality of pollen will have a significant impact on pollination success in self-incompatible species (Aizen and Harder 2007). In this way, the flowering phenology have a crucial role in the structuring these interactions and the reproductive outputs in a sympatric condition of species with similar pollination niche.

This study aimed to investigate the temporal distribution of flowering of three oil-producing Iridaceae species and the differences in bee performance based on pollen deposition on the stigmas of them between oil- and pollen-collecting bees. This result will contribute to a better description of the realized pollination niche of these plant species and their reproductive outputs in a geographical co-occurring scenario in Pampean grasslands and the effective role of floral oil in determining predicted floral syndrome.

2 Material and methods

2.1 Study area and species

The study site is located in the Serra do Sudeste region on the Southern Brazilian Campos at Rio Grande do Sul state, Southern Brazil, and is characterised by the prevalence of rainy and cold winters (including some days with temperatures below zero) and dry and hot summers (often above the 30 °C). This region is geomorphologically complex, formed mostly during the Precambrian with elevation ranges not reaching 350 masl. This area is characterised by subtropical grasslands and rock outcrops with a high diversity of oil-producing species of Iridaceae (Overbeck et al. 2007; Eggers et al. 2020) (Fig. 1).

Cypella herbertii (Lindl.) Herb., *Kelissa brasiliensis* (Baker) Ravenna, and *Herbertia pulchella* Sweet were chosen to assess the different levels of specialisation in oil bee pollination. Despite their colour differences, these species are quite similar about flower size. In addition, two of them are considered critically endangered or vulnerable, according to the Red list of threatened species of the Rio Grande do Sul state. *Cypella herbertii* is mainly visited by oil bees (especially *Arhysoceble picta* (Friese, 1899), *K. brasiliensis* is visited by both oil- and pollen-collecting bees, and *H. pulchella* is presumably less specialised in oil bee pollination, being visited

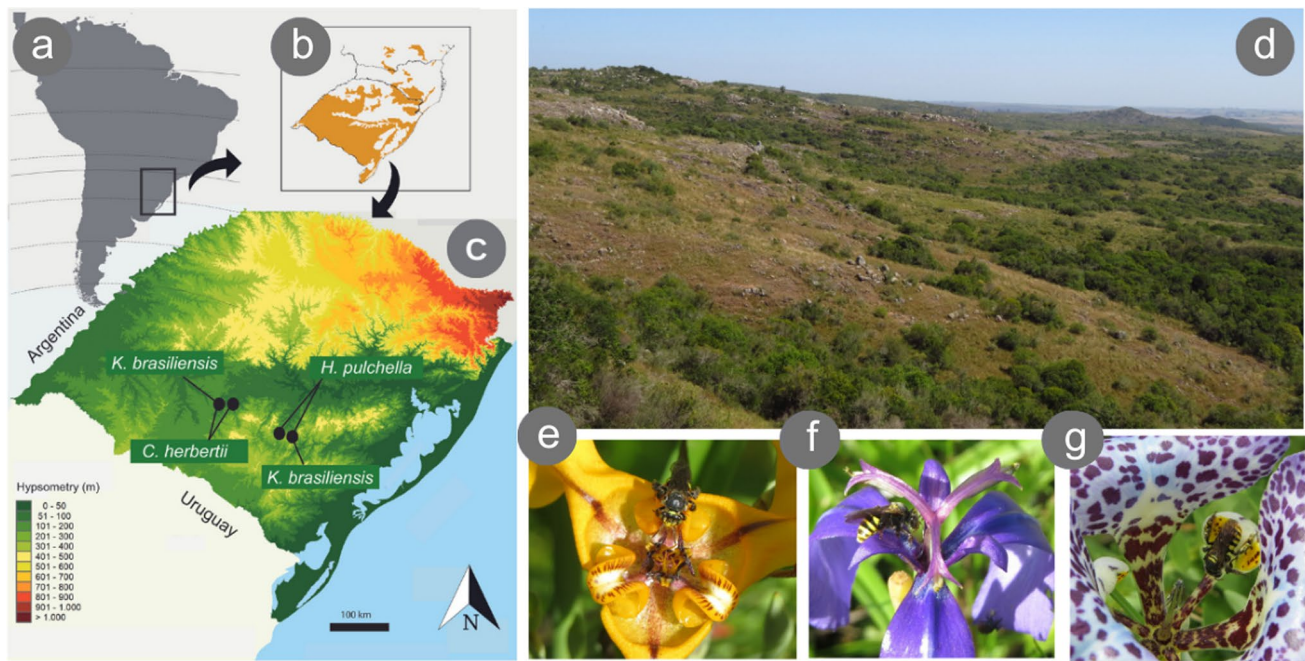


Fig. 1 Map of localization of studied area. **A** Localization of studied area in South America, **B** The Southern grasslands of Brazil distribution, **C** Rio Grande do Sul state with relief characterization and the populations studied locations (modified from EMBRAPA- SEPLAG/DEPLAN – 06/2020), **D** A typical environment of the studied areas, **E, F, G**) Flowers of *C. herbertii*, *H. pulchella* and *K. brasiliensis*, respectively, visited by *A. picta* oil-bee

by a great range of pollen-collecting bees. During the peak flowering season, we sampled two populations per species. The bee species composition and floral visit frequency used in this study were obtained from Oleques et al. (2020) results.

3 Flowering phenology

The study was conducted during the flowering season from September 2016 to April 2017. Periods before September and after April were monitored to verify the complete absence of flowers. We recorded the flowering phenology of the three species studied through direct observation of the number of individuals presenting flowers in each sample species population (more than 100 individuals for each species) once every 15 days during the study period. We observed the number of flowers for each individual plant, and the flowering intensity for each sample period was considered to be the proportion of flowering individuals in the sampled population.

4 Floral visitors and pollen deposition on the stigma

The bee species observed in this study were the same as those in Oleques et al. (2020), and they were divided into the following two functional groups: oil-collecting bees

(OB) and pollen-collecting bees (PB). Moreover, for this study, we made new records of bee visitation in the same plant populations cited by Oleques et al. (2020) during the flowering season of the species in 2021. To assess the pollen deposition all buds were previously bagged, and the flowers were emasculated before the experiment to prevent pollen from the same flower on the stigma surface. After a single legitimate bee flower visit (when the bee contacted anthers and stigmas) from both bee functional groups, the stigmas from flowers of different individuals of the three plant species were removed and we recorded the total and conspecific pollen grains deposited on them totalizing 69 pollen-stigmas samples from 69 bees (*C. herbertii*, oil bees = 19 flowers, pollen bees = 6 flowers; *H. pulchella*, oil bees = 10 flowers, pollen bees = 16 flowers; *K. brasiliensis*, oil bees = 7 flowers, pollen bees = 11 flowers). The stigmas were placed in small plastic tubes containing 1 mL of distilled water and macerated with a glass stick. An aliquot was inserted into a micropipette, and a Neubauer chamber was covered with a blade. This sample were observed under an optical microscope to count pollen grains in the chamber quadrants differing co- and heterospecific pollen grains, as described by De Oliveira (2016). The procedure for determining pollen content in the Neubauer chamber for counting was repeated three more times, totalling four counts for each sample. The pollen grains counts were used as an indicative of amount pollen on stigmas surface.

We evaluated the total number of pollen grains deposited on the stigma surface (tp) and the conspecific pollen grains (cp) and calculated the proportion of cp/tp for each species studied.

To calculate the “pollinator performance index” (PPI) of pollen- and oil-collecting bees (ij) for each plant species, we consider both visitation frequency results from Oleques et al. (2020) and the conspecific pollen deposition on stigma data obtained in this study, as follows:

$$PPI_{ij} = (\text{mean } cp/tp_{ij} \times \text{mean of visitation frequency}_{ij})/n_{ij}$$

where cp is the conspecific pollen deposited, tp is the total pollen grains deposited from both bee functional groups, and n is the number of bee species of each functional group. In addition, we utilized the bee species richness of each bee group (n_{ij}) acting as a pollinator in each plant species recorded in Oleques et al. (2020).

5 Pollination limitation

To better understand the role of pollinators in the reproductive outputs of the studied species, we

used data from Oleques et al. (2020) to calculate the pollination limitation index proposed by Duan et al. (2007) using the following formula:

$$PL = 1 - P_n/P_m$$

where P_n denotes the number of fruit set (fruits/marked flowers) from natural pollination and P_m is the number of fruit set from manual cross pollination. The results varied from 0 to 1, where 0 indicates the absence of pollination limitation and 1 indicates the highest level of pollination limitation.

6 Data analysis

The flowering phenological pattern was verified through circular statistics, in which the year was considered as a circumference and the intensities of flowering were estimated based on angles producing a mean vector angle (u). The non-random flowering pattern was tested using the Rayleigh test (z) and pair-comparing between the three species through the Hotteling test (F) using Oriana 4 software (Kovach Computing Services 2011).

To verify the effects of the different bee functional groups on the amount of pollen deposition (total and conspecific) for each plant species, we compared the mean values of pollen grains deposited using a GLM test considering the plant species and bee functional group as fixed effects and the total pollen (tp) and conspecific pollen (cp) as dependent

variables with a negative binomial distribution (used after an overdispersion test of data). After this, we calculated the ratio cp/tp and tested the difference using GLM test with a binomial distribution of data. To analyse binary data related to fruit sets obtained from hand-crossed pollination and natural pollination treatments, data were fitted to GLMMs, considering pollination treatments as fixed effects and individual plants as random effects with a Bernoulli distribution. All analyses were conducted using R version 4.0.3 (R development Core Team 2020).

7 Results

7.1 Flowering phenology

Flowering events were observed from the second week of September to later April with a seasonal pattern for the three species (*Cypella herbertii*, $u = 320.995^\circ$, $z = 57.61$, $p < 0.001$; *Kelissa brasiliensis*, $u = 269.987^\circ$, $z = 96.31$, $p < 0.001$ and *Herbertia pulchella*, $u = 292.756^\circ$, $z = 90.99$, $p < 0.001$). The mean vector angle differed significantly between *C. herbertii* and *K. brasiliensis* ($f = 2.36$, $p = 0.0025$) and *H. pulchella* and *K. brasiliensis* ($f = 2.36$, $p = 0.005$). *C. herbertii* and *H. pulchella* did not differ significantly ($f = 1.96$, $p = 0.16$) (Fig. 2).

8 Pollen deposition on the stigma

The mean values of total and conspecific pollen grains deposited on stigmas differed among the plant species and the values were higher by pollen bees than oil bees in two of the three plant species studied (GLM, total pollen, $\chi^2 = 10.72$, $df = 1$, $p = 0.001$; GLM, conspecific pollen, $\chi^2 = 19.66$, $df = 2$, $p = 0.0005$) (Fig. 3). Within each plant species, a significant difference between oil and pollen bees contribution on pollen on stigmas was found in *Cypella herbertii* (GLM, total pollen, $\chi^2 = 7.67$, $df = 1$, $p = 0.0056$; conspecific pollen, $\chi^2 = 8.09$, $df = 1$, $p = 0.004$) and *Herbertia pulchella* (GLM, total pollen, $\chi^2 = 4.17$, $df = 1$, $p = 0.041$; conspecific pollen, $\chi^2 = 11.32$, $df = 1$, $p = 0.008$). The two functional bee groups was not different in pollen deposited on stigmas in *Kelissa brasiliensis* (GLM; Total pollen, $\chi^2 = 0.39$, $df = 1$, $p = 0.53$; conspecific pollen, $\chi^2 = 0.01$, $df = 1$, $p = 0.97$). The conspecific/total pollen ratios (cp/tp) calculated for each species were very similar between oil and pollen bees (Murúa 2020) (above 0.75) with non-difference between the two bee functional groups (GLM, $f = 0.68$, $df = 1$, $p = 0.41$). However, a significant difference in the cp/tp ratio deposited on stigmas was observed among the three plant species (GLM, $f = 9.70$, $df = 2$, $p = 0.008$).

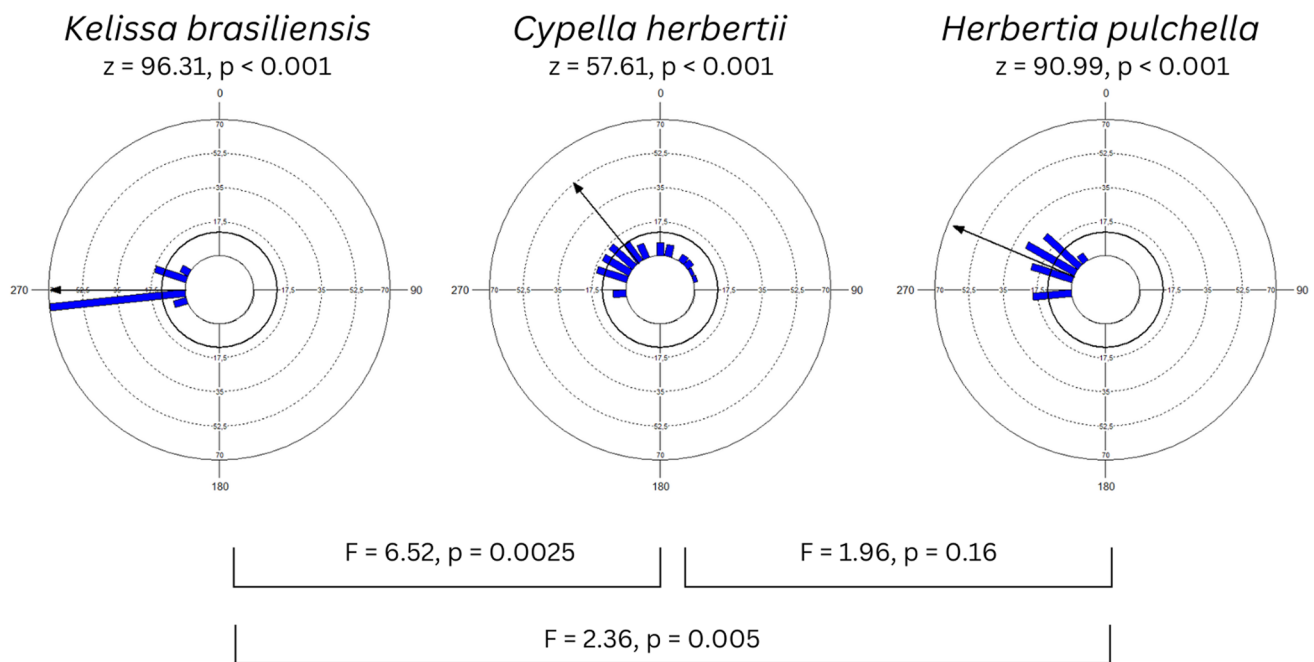


Fig. 2 Circular histogram representing the flowering phenology of *Kelissa brasiliensis*, *Cypella herbertii* and *Herbertia pulchella* respectively. The intensities of flowering are represented by the columns height in the specific angular scale measured each 15 days. The arrows indicate a mean vector angle of the flowering period. Statistical differences among the plant species are indicate above

9 Pollinator performance index (PPI)

The performance of oil bees was higher than pollen bees in all species studied. The magnitude of this difference was higher in *H. pulchella* ($PPI_{pollen\ bees}=0.013$, $PPI_{oil\ bees}=0.053$) and in *C. herbertii* ($PPI_{pollen\ bees}=0.087$, $PPI_{oil\ bees}=0.12$) while in *K. brasiliensis* we recorded similar values ($PPI_{pollen\ bees}=0.016$, $PPI_{oil\ bees}=0.02$) (Fig. 4).

10 Pollination limitation

Fruit set from natural pollination differed significantly from hand-crossed pollination (HCP) with lower natural fruit set (NP) mean values in all species (*H. pulchella*, HCP=0.58, NP=0.38, $\chi^2 = 4.618$, $df = 1$, $p = 0.031$; *C. herbertii*, HCP=0.67, NP=0.42, $\chi^2 = 14.086$, $df = 1$, $p = 0.02$ and *K. brasiliensis*, HCP=0.67, NP=0.36, $\chi^2 = 13.703$, $df = 1$, $p < 0.01$). The pollination limitation index (PL) of all plant species studied presented moderated values below 0.5 (*H. pulchella*, PL=0.37; *C. herbertii*, PL=0.41 and *K. brasiliensis*, PL=0.46).

11 Discussion

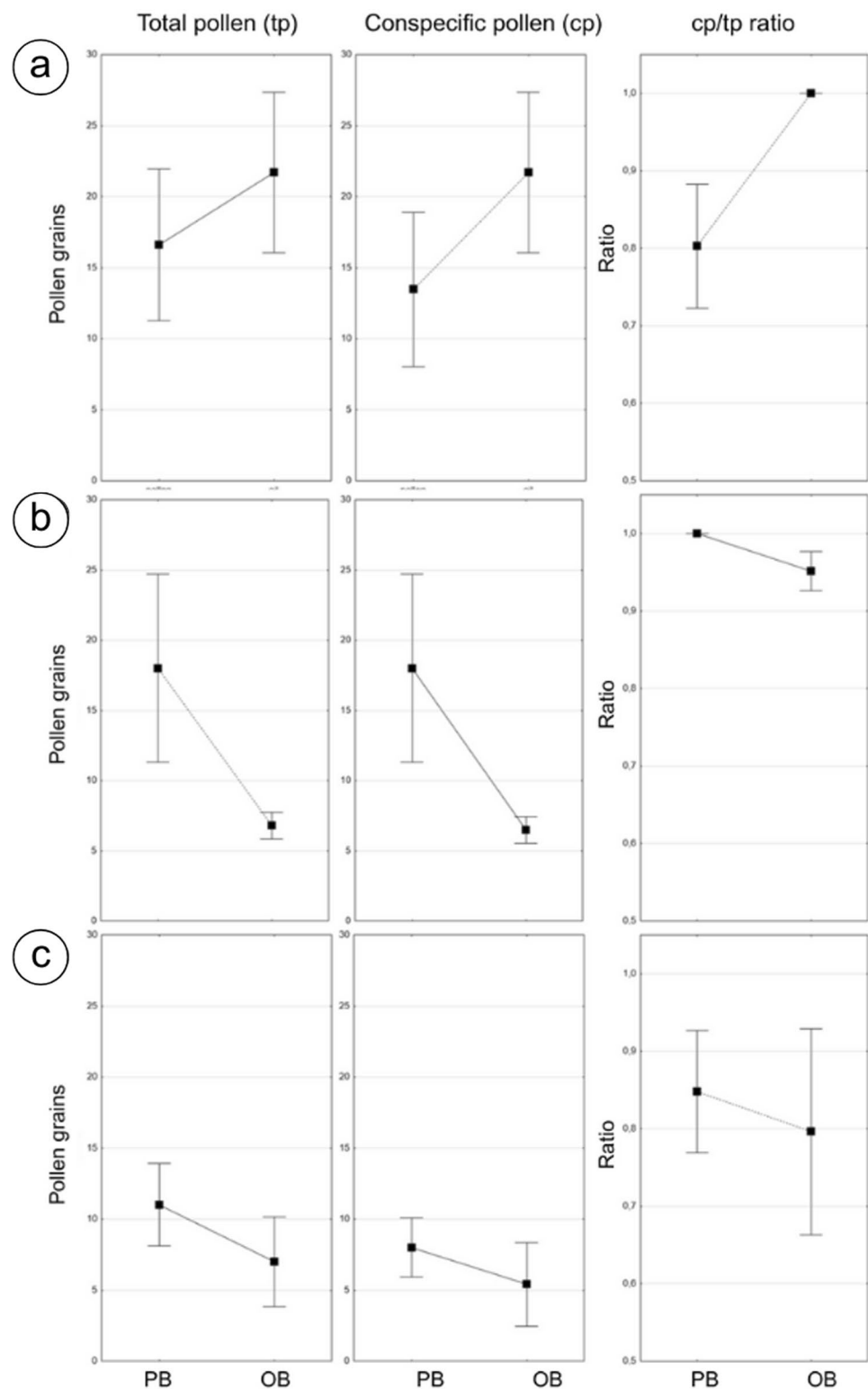
This study contributes to the knowledge of a very specialized plant-pollinator system, and shows that two of the three species studied here are part of a very conservative pollination

niche according to literature about these highly specialized plant-oil bee interactions (Vogel 1974; Buchmann 1987; Pauw 2006; Cocucci 2001) while another one presented a widening of its pollination niche.

Oleques et al. (2020) already inferred the hypothetical existence of three different realized pollination niches through differential visitor frequency and pollen export between pollen and oil bees in these species: a pollen bee visits prevalence in *H. pulchella*, the oil bee visits prevalence in *C. herbertii*, and a mixed pollination system with the two bee groups visiting *Kelissa brasiliensis*. However, our results indicated that oil bees were more effective pollinators in *H. pulchella* as well as *C. herbertii*, contributing to an overlapping of the pollination realized niche between them, whereas the two bee functional groups (oil and pollen bees) were equally efficient in *K. brasiliensis*, widening its pollination niche breadth. In this way, the hypothetical pollination niches described in the previous study by Oleques et al. (2020) were partially corroborated.

The flowering pattern of the species studied had a fundamental role in temporal pollinator partitioning. There was a temporal segregation of *K. brasiliensis* from the other two species observed during this study. *Herbertia pulchella* and *C. herbertii* overlapped their flowering periods with slight variation in flowering peaks (Fig. 2). Considering pollinators as resources, the flowering phenological pattern observed could lead to wide bee exploitation from both functional bee groups by *K. brasiliensis*,

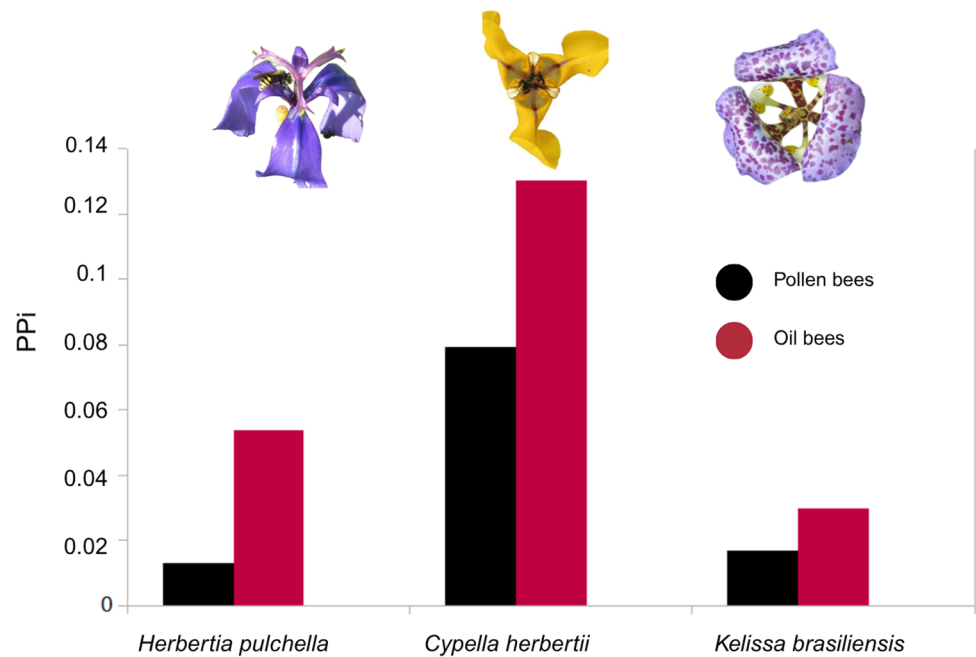
Fig. 3 Estimated values (mean $\pm$ s.e) of total pollen (*tp*), conspecific pollen grains (*cp*) and the *cp/tp* ratio deposited on stigmas by pollen (PB) and oil bees (OB). **a** *Herbertia pulchella*, **b** *Cypella herbertii*, and **c** *Kelissa brasiliensis*



whereas *H. pulchella* and *C. herbertii* experienced higher oil bee partitioning. In contrast to the competitive effects usually associated with this scenario (Johnson et al. 2022), the flowering overlap between *H. pulchella* and *C. herbertii* illustrates a good example of the non-interference of

interspecific pollen in plants with a very similar pollination niche that is neither a potential facilitative interaction case (Ghazoul 2006) leading to a neutral effect on reproductive outputs, according to Albor et al. (2022) hypothesis. This fact was supported when we observe the moderate

Fig. 4 The pollinator performance index (*Ppi*) of pollen and oil bees for the three Iridaceae species studied



pollination limitation values observed in the three species, particularly *H. pulchella* and *C. herbertii* contrasting with some degree of pollen or pollination limitation in other studies in this particular pollination system (Cosacov et al. 2008; Tadey 2012).

The flower morphology and oil bee behaviour observed during the visits in *H. pulchella* and *C. herbertii* may be associated with the neutral effect of temporal and pollination niche overlapping (Botes et al. 2008). It was evident that oil bees exclusively collected oil in *C. herbertii*, and the squeezed space in the tepals to access the oil secretion structures (elaiophores) promoted anthers and stigma contact with the dorsal part of the oil bee body. Contrasting with this, oil bees actively harvested pollen and oil during the visits to *H. pulchella* flowers leading to contact with the anthers and stigma in their ventral body parts. The *cp/tp* ratio was higher in oil bees, which contributed to the higher values of the *PPi* of the oil bees in *H. pulchella* and *C. herbertii* and similar values in *K. brasiliensis*. In addition, there was a difference in the number of species of both bee groups acting as pollinators, with a prevalence of pollen bee species and some social species with higher visit frequency. When we observe the position of the anther and stigma in the plant species studied, their proximity could contribute to the effective input of oil bees during pollen harvesting and also to the contribution of the pollen bees. Despite of this, in our studied system, three oil bee species outperformed the 16 different pollen bee species (Oleques et al. 2020). Some indications of oil bee performance were provided by Boff et al. (2018), who pointed out the higher efficiency of oil bees than pollen bees; however, this result was related

to the higher frequency of oil bee visits, contrasting with our results.

Besides that, we can infer a higher floral constancy promoted by oil than pollen bees by looking at the difference in conspecific and total pollen deposited (Fig. 3). Oil bees presented higher values of *cp/tp* ratio than pollen bees particularly in *H. pulchella*. Narrow trophic niches, or oligolectic behaviour, observed in several oil bee species, particularly on Tapinotaspidini, have been related (Schlindwein 1998; Minckley and Roulston 2006; Aguiar et al. 2017) and could be associated with this floral constancy observed in *H. pulchella* and *C. herbertii* and their higher pollinator performance. However, solitary and oligolectic pollen bees were observed on *Cypella herbertii* flowers while *H. pulchella* and *K. brasiliensis* were also visited by social and generalist pollen bees, such as *Apis mellifera* (Linnaeus, 1758), *Trigona spinipes* (Fabricius, 1793) and *Mourella caerulea* (Friese, 1900) (Kleinert and Giannini 2012) that can be associated to differences in *cp/tp* and the *PPi* of pollen bees among the plant species. We need to highlight that our pollen analysis using distilled water instead of a glycerinated lactic solutions could be associated with discrepancy of pollen counts and the overdispersion observed.

In addition, the diversified Tapinotaspidini oil bee fauna is recognised in open and xeric vegetation types, similar to the study area (Aguiar et al. 2020; Aguiar et al. 2023; Camargo et al. 2023). However, the few oil bee species observed in this study could be the result of some constraint in the geographic distribution of the oil bees. Some extrinsic factors, such as land use intensification to soybean cultivation, common in the studied area (Baeza et al.

2022), could be associated with changes in oil bee richness, disrupting some specialised plant–pollinator systems in Southern South America (Marrero et al. 2014; Graffigna et al. 2021) and affecting the realized pollination niche of oil secreting plant species. It is worth mentioning that even with our low oil bee richness compared with pollen bees, their pollinator performance was higher than pollen bees observed in *H. pulchella* and *C. herbertii* (Fig. 3).

However, pollen bees could also contribute to pollination of these species, ensuring the reproductive outputs in populations where oil bees are not present or not attracted for these plants in a plant community enhanced with other oil flower species (Steiner and Whitehead 1996; Manning and Goldblatt 2002). In fact, in some cases, the evolution of specialized pollination is not associated with an obligated fitness trade-off with the effectiveness of a pollinator group, leading to a negative effect of marginal effective another pollinator group (Armbruster 2017).

This study highlights that both pollen and oil bees are important pollinators of the studied species. Nevertheless, they differ in visit frequency and pollinator performance. Pauw et al. (2020) describe an alternative perspective to Stebbins's most effective pollinator principle (Stebbins 1970) by emphasising the importance of the least effective pollinator on the evolution of floral traits resulting from fluctuation in the most effective pollinators. Prevalence of pollinator efficacy or performance as selective pressure instead of frequency or weak trade-off related to adaptation to the least important pollinator. Therefore, oil secretion in the studied species could be present until now by its adaptive function in the past enhancing pollination rates in their populations.

Finally, our data suggest that this particular system exhibited strong pollination niche conservatism in two of the three species, as predicted by the syndrome of floral traits. However, further studies are needed on the geographical distribution of the studied species to verify variations in oil bee performance and some correlation with floral traits and oil secretion.

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Author contributions SS Oleques and RS Avila Jr developed the theoretical formalism, carried out the field experiment and the statistical analysis. SS Oleques and RS Avila Jr wrote the manuscript with support from TT Souza-Chies. TT Souza-Chies supervised the project.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval Not applicable.

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